HYOID AND VENTRAL GILL ARCH MUSCULATURE IN OSTEOGLOSSOMORPH FISHES

BY

PETER HUMPHRY GREENWOOD

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ABSTRACT

The ventral hyoid and gill arch musculature in several representatives of all osteoglossomorph families is described and compared. The results of this survey show clearly the unusual specializations of the Mormyridae, and add evidence to the

suggested relationships of the Mormyridae to the Notopteridae. The Osteoglossidae and Pantodontidae show a different (and more usual) type of specialization. The Hiodontidae have a basic teleostean pattern in the hyoid muscles, not far removed from the *Amia* pattern.

Based on these and other characters, a new intragroup classification is suggested for the Osteoglossomorpha (including the reduction of the Gymnarchidae to subfamilial status within the Mormyridae).

INTRODUCTION

Although the ventral gill arch and hyoid musculature has been described (with varying degrees of thoroughness) for some osteoglossomorph fishes (Holmquist, 1911; Munshi, 1960; Bishai, 1967; Nelson, 1969), to date there has been no fully comparative account of these muscles; furthermore, only a few species have been investigated.

The present study is an attempt to fill both these gaps, and is part of a continuing investigation of intragroup relationships among the Osteoglossomorpha. That the musculature might provide some information on this subject is suggested by Nelson's (1969) examination of dorsal and ventral gill arch muscles in certain notopterid, mormyrid, osteoglossid and hiodontid species. Nelson's results are somewhat equivocal (and some are modified by my study), but if the hyoid musculature is also taken into account, a rather different picture emerges.

Nomenclature. For the gill arch muscles I have followed the nomenclature used by Nelson (1967 and 1969) which, in turn, was based on the terminology of Vetter (1878) and Edgeworth (1935).

The hyoid muscles provide something of a nomenclatural problem. The major muscle connecting the hyoid bar with the lower jaw is generally called either protractor hyoideus or geniohyoideus. (See Holmquist, 1911; Dietz, 1912, Edgeworth, 1928 and 1935; Munshi, 1960, and Osse, 1969 for discussions of this problem). It is clear that on grounds of homology and ontogeny (Edgeworth, *op. cit.*) the muscle should not be called a geniohyoideus in teleost fishes.

Associated with this muscle there is usually a much smaller, transverse muscle, the so-called intermandibularis, which lies anteriorly between the rami of the jaws.

As Holmquist (*op. cit.*) suggested, and Edgeworth (1928) later demonstrated embryologically, the protractor hyoideus is a compound muscle derived from an intermandibularis component anteriorly (the so-called posterior intermandibularis as distinct from the transverse anterior intermandibularis), and an interhyoideus component posteriorly.

Among the osteoglossomorphs studied, the protractor hyoideus shows, at least superficially, varying degrees of complexity or unity. In many osteoglossoids it appears to be a single muscle, in hiodontids a single muscle obviously of compound origin, and in mormyrids and notopterids a group of distinct muscles. Thus, in osteoglossoids I shall refer to this muscle as the protractor hyoideus, and in the notopterids and mormyrids the components will be named (*viz.* interhyoideus and posterior intermandibularis). The use of the term "protractor" here is purely

nominal and does not imply any functional attributes (see Osse, *op. cit.*). In most species the anterior intermandibularis is clearly identifiable despite its great variation in size and area of attachment.

There is general agreement on the nomenclature for that part of the constrictor hyoideus ventralis associated with the branchiostegal rays, namely the hyohyoideus, and that term is used in this paper.

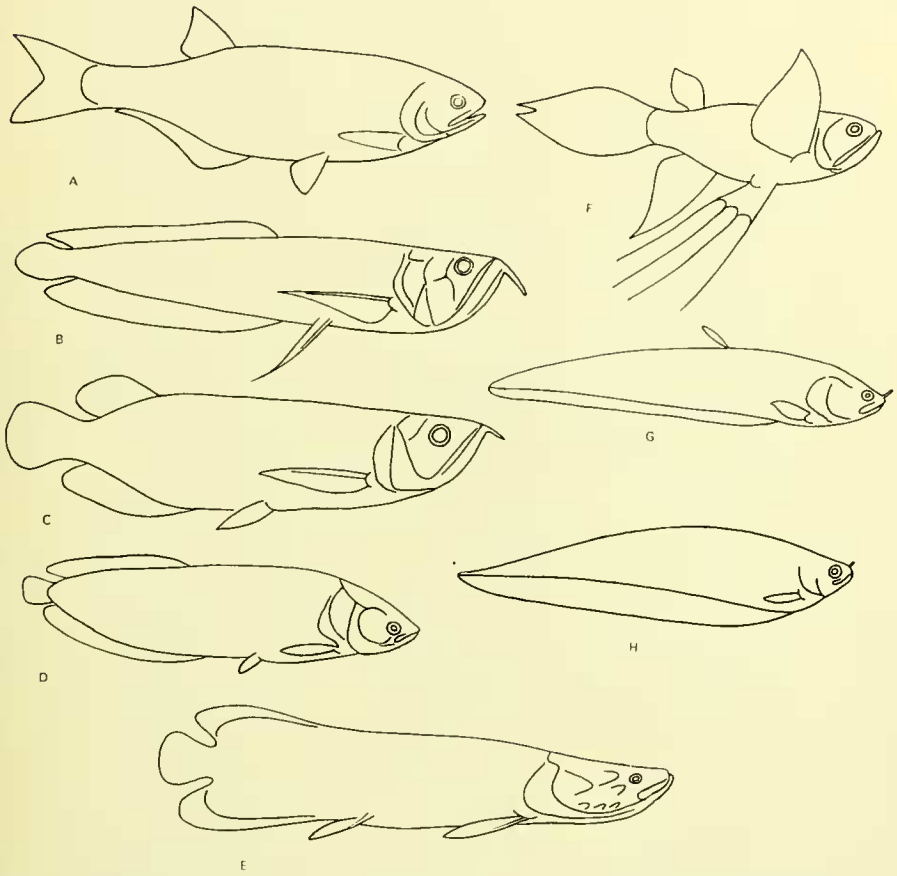


FIG. 1. Outline drawings, not to scale, of: A. *Hiodon alosoides*. B. *Osteoglossum bicirrhosum*. C. *Scleropages leichardti*. D. *Heterotis niloticus*. E. *Arapaima gigas*. F. *Pantodon buchholzi*. G. *Papyrocranus afer*. H. *Xenomystus nigri*.

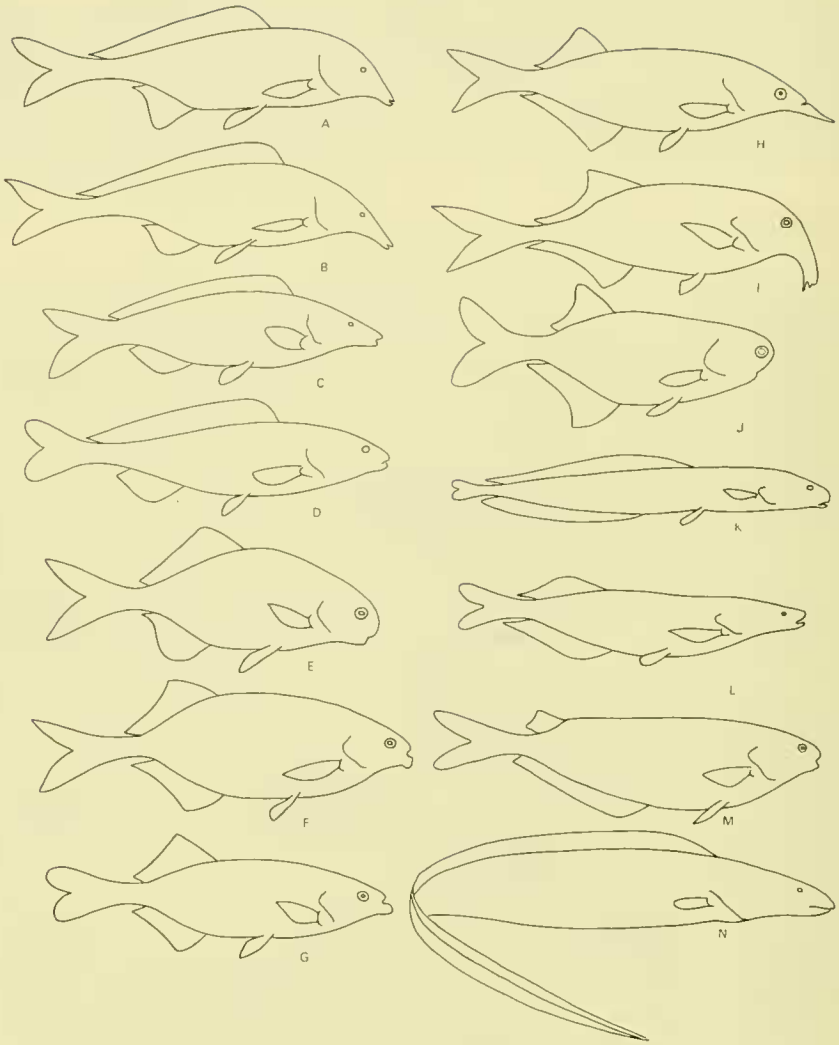


FIG. 2. Outline drawings, not to scale, of various mormyrid species: A. *Mormyrus kannume*. B. *Mormyrus caschive*. C. *Mormyrus lacerda*. D. *Mormyrus hasselquisti*. E. *Cyphomyrus discorhynchus*. F. *Marcusenius cyprinoides*. G. *Marcusenius victoriae*. H. *Gnathonemus longibarbis*. I. *Campylomormyrus elephas*. J. *Petrocephalus bane*. K. *Isichthys henryi*. L. *Mormyrops anguilloides*. M. *Hyperopisus bebe*. N. *Gymnarchus niloticus*.

MATERIALS AND METHODS

Dissections were made on the following specimens; for most species dried skeletons or alizarin transparencies were also available.

Species	B.M.(N.H.) register number	Standard length, mm.
Hiodon alosoides	1965.7.2 : 1–3	185, 150, 136
Hiodon alosoides	1965.11.23 : 1–8	143, 124, 110, 108, 105
Osteoglossum bicirrhosum	1926.10.27 : 1–2	340, 286
Scleropages leichardti	1966.9.23 : 5	200
Scleropages formosus	1966.9.5 : 1	60
Heterotis niloticus	unregistered	300
Arapaima gigas	unregistered	245
Pantodon buchholzi	1913.3.12 : 1	67
Papyrocranus afer	1969.3.26 : 27	196
Papyrocranus afer	unregistered	290, 225
Xenomystus nigri	unregistered	146, 145, 140, 140, 130
Xenomystus nigri	unregistered	140
Xenomystus nigri	unregistered	145
Notopterus kapirat	1931.7.20 : 9–17	174, 167, 155
Notopterus kapirat	1938.2.22 : 11	213
Mormyrus kannume	unregistered	203
Mormyrus lacerda	1965.3.15 : 316–320	260, 210, 200
Mormyrus hasselquisti	unregistered	240
Cyphomyrus discorhynchus	1966.7.29 : 2–4	137, 137, 125
Marcusenius cyprinoides	1961.12.1 : 48–74	150, 132
Marcusenius victoriae	1961.6.13 : 16	130
Marcusenius victoriae	1962.2.6 : 26	152
Gnathonemus longibarbus	1928.5.24 : 2	150
Campylomormyrus elephas	1928.7.30 : 3–4	136, 134
Campylomormyrus elephas	1919.9.10 : 61	154
Petrocephalus bane	1907.12.2 : 231–232	150, 150
Petrocephalus bane	1905.3.15 : 1–2	110, 104
Petrocephalus bane	unregistered	112, 112
Petrocephalus catostoma	1961.6.21 : 7–18	76, 73, 72, 68, 60
Isichthys henryi	1958.9.18 : 5–6	200
Isichthys henryi	unregistered	270, 240
Mormyrops deliciosus	1969.3.26 : 28	235
Mormyrops anguilloides	unregistered	205
Hyperopisus bebe	1948.6.30 : 1–4	190, 145, 140, 140
Hyperopisus bebe	1969.3.25 : 34	195
Gymnarchus niloticus	1969.3.26 : 49	370
Gymnarchus niloticus	1948.6.30 : 21	330
Gymnarchus niloticus	1902.11.10 : 56	290

Species	B.M.(N H.) register number	Standard length mm.
Gymnarchus niloticus	1953.7.10 : 5	400
Amia calva	unregistered	48 (head only)
Albula vulpes	1949.11.29 : 1–4	177, 157, 152
Elops saurus	1961.8.31 : 45	134

ABBREVIATIONS USED IN TEXT FIGURES

A: Articular
AIM: anterior intermandibularis muscle
Apn: aponeurosis
ASCh: articular surface for ceratohyal on 1st basibranchial (Nelson's [1968] terminology)
AT: anterior transversus muscle
Bb 1–3: basibranchial, 1st–3rd arch
BhTp: basihyal tooth plate
BrR: branchiostegal ray
BrM: branchiostegal membrane
Bt: basihyal, and its tooth plate, with connective tissue cover
CbI–V: ceratobranchial (arches I–V)
CbM: muscle connecting 4th and 5th ceratobranchials
Ch: ceratohyal
Chc: cartilaginous part of ceratohyal
ChUh: muscle between ceratohyal and urohyal
CL: cleithrum
CT: connective tissue surrounding lateral and ventral edges of basihyal and its anterior tooth plate
CTM: connective tissue mass covering posteroventral end of basihyal tooth plate and articulation of the urohyal
D: dentary
Gr: gill rakers
HaBM: hypaxial body musculature
HbI: hypobranchial (arch 1)
HbII: of second arch
Hhy: hyohyoideus muscle
Hhya: anterior portion of hyohyoideus muscle
Hp: hypohyal
Hpic: hypohyal (cut through)
IH: interhyoideus muscle
IHhy: inferior hyohyoideus muscle
Ihyi: interhyoideus muscle, inner (medial) division
Ihyim: interhyoideus muscle, innermost division
Ihyl: interhyoideus muscle, lateral division
Ihyvl: interhyoideus, ventrolateral muscle
IOp: interoperculum
L: ligament from basihyal tooth plate (to urohyal)
LUh: ligament from urohyal to hypohyals
Max: cut end of maxilla
Mb: mental barbel
MC: mental cartilage
Ob 1–3: obliquus muscle (1st–3rd gillarches)
PhCA and P: external and internal pharyngocleithralis muscles
PIM: posterior intermandibularis muscle
PIMm: lateral muscle bands of posterior intermandibularis muscle
PIMms: posterior muscle slips of posterior intermandibularis muscle
PIMt: tendinous portion of posterior intermandibularis muscle
POp: preoperculum
PrH: bony process from second hypobranchial
Q: quadrate
R: rectus muscle
RC: rectus communis muscle
S: sulcus between posterior intermandibularis and interhyoideus muscles
Sc: lateral line sensory canal in dentary
SH: sternohyoideus muscle
SHl: sternohyoideus, lower division
SHu: sternohyoideus, upper division
SHhy: superior hyohyoideus muscle
SOpBr: subopercular branchiostegal rays
T: teeth
Thy: tendon from interhyoideus muscle
Thy l: tendon from lateral division of interhyoideus muscle
TSH: tendon from sternohyoid
TSHBb: tendon from sternohyoid muscle to second basibranchial
Uh: urohyal
I–V: gill arches

Family **HIODONTIDAE**

Hiodon alosoides (Rafinesque)

(Text-fig. 1A)

Protractor hyoideus complex (text-fig. 3). Although at first sight there appears to be only a single muscle forming the floor of the mouth, closer examination of fibre direction shows that it is a compound of: (1) a large posterior sheet (fibres running obliquely anteromedially towards the median aponeurosis) (2) a much smaller, oval sheet anteriorly (fibres transverse to postero-medial) and (3) on each side, joining the former two sheets, a narrow elongate muscle with almost longitudinally directed fibres.

The various components are tightly joined through narrow aponeuroses, and there is some exchange of fibres between the different muscles.

The posterior sheet originates on the ceratohyal, with a few fibres stemming from the bases of the fourth and fifth branchiostegal rays; a fine median aponeurosis is visible along the entire length of the muscle. A sheet of dense connective tissue joins the lateral margins of this muscle to the ventral margin of the dentary on each side. Anteriorly the muscle ends aponeurotically on a broad sheet of connective tissue extending between the rami of the jaw, and lying dorsal to the other muscles of the protractor hyoideus complex. The posterior sheet joins, aponeurotically, the oval median muscle and, on each side, the slender elongate muscles. Thus, it has no direct insertion onto the lower jaw. In contrast, both the median oval and the lateral rectangular muscles attach directly to the median ventral face of each dentary.

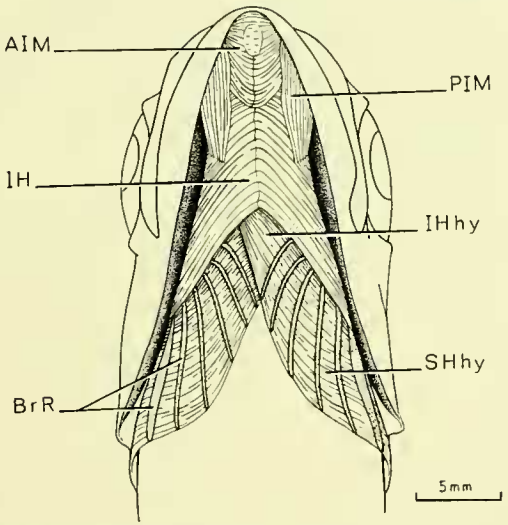


Fig. 3. *Hiodon alosoides*: ventral hyoid muscles after removal of the skin.

From its innervation (a branch of the hyohyoideus VII nerve) and its origin on the ceratohyal, I would identify the posterior muscle sheet as the conjoined left and right interhyoidei. The anterior complex of three muscles (all innervated by a branch of the mandibular V nerve) would seem to be, from their topographical positions, an unpaired median anterior intermandibularis (the oval muscle) and a posterior intermandibularis divided by the backward extension of the anterior intermandibularis.

There is a striking similarity between the protractor hyoideus complex in *Hiodon* and the condition found in *Amia*, *Elops* and *Megalops* (personal observations on *A. calva*, *E. saurus* and *M. cyprinoides*; also Allis, 1897; and Liem, 1967). In all, there is a single anterior intermandibularis, paired (but medially joined in *Amia* and in the elopoid genera) posterior intermandibulares (the geniohyoideus of Liem *op. cit.*), and an extensive, paired interhyoideus. *Hiodon* differs from the others chiefly in having the interhyoid components more compact and closely associated with each other. Liem (*op. cit.*) describes musculose insertions of all components onto the gular plate, but I was unable to confirm this in my own dissections. Indeed, the muscles seem to be completely free from the gular plate which is attached only to the connective tissue covering the muscles. The protractor hyoideus in all four genera differs markedly from that in *Albula* (personal observations; see also Holmquist, 1911; Liem, *op. cit.*), which represents a relatively specialized condition (see also p. 44 for further comments on *Albula* and *Gymnarchus*).

Hyohyoideus. The superior (interbranchiostegal) part of this muscle is weakly developed, and is largely tendinous (text-fig. 3). The inferior part is much better developed. It originates on the first (*i.e.* lowermost) branchiostegal ray of each side and inserts, mainly, on the hypobranchial of the opposite side (left muscle lying below the right). From the medial side of each inferior hyohyoideus a short slip of muscle inserts, through a long shared tendon, onto the basihyal plate about half way along its length. The tendon is closely applied to the ventral face of the basihyal plate even before its actual point of insertion.

Sternohyoideus (text-fig. 4). The main, ventrally situated part of this muscle inserts directly onto the urohyal, and has its origin aponeurotically, from the ventral body musculature. No ventral part of the sternohyoid originates on the cleithrum, but there is a smaller dorsal component originating on the horizontal limb of that bone. From about the middle of this upper segment a broad-based, almost completely tendinous slip runs forward and upwards to insert on the basibranchial of the second gill arch. Apart from this link, there is no connection between the sternohyoideus and the branchial skeleton. The possible significance of this tendon in the evolution of the tendon-bones and ventral bony processes associated with the second gill arch in all other osteoglossomorphs (see Greenwood, Rosen, Weitzman, and Myers, 1966; Nelson, 1968) will be discussed later (page 51).

Ventral gill arch muscles (text-fig. 4). Well-developed *obliqui* muscles are present on the first three gill arches. The *rectus communis* is a large muscle at its origin from the ceratobranchial of the fourth arch, but it becomes tendinous as it passes below the medial end of the second obliquus, and remains tendinous until its insertion on the second basibranchial. This tendon also attaches to a small process from the

second hypobranchial, and is very closely associated with, but distinct from the ligament joining the first basibranchial to the second hypobranchial. A poorly-defined *rectus* is present between the fourth ceratobranchial and the third hypobranchial; it is barely distinguishable from the larger and laterally situated rectus communis. Well developed *anterior* and *posterior transversi* link the proximal ends of the fourth and fifth ceratobranchials respectively.

External and internal *pharyngocleithrales* are present. The origin of the external division is medial to the sternohyoideus, but the internal muscle originates from the cleithrum at the same level as the sternohyoideus, and superficially resembles a division of that muscle.

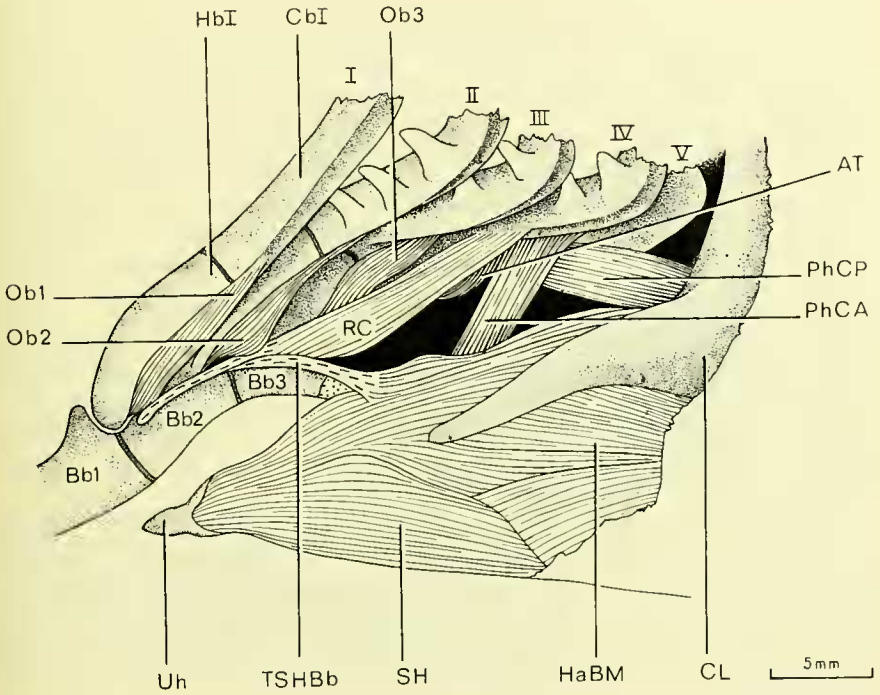


FIG. 4. *Hiodon alosoides*: ventral gill arch musculature and sternohyoideus in left lateral view.

Family **OSTEOGLOSSIDAE**

Subfamily **OSTEOGLOSSINAE** (Nelson, 1968)

Osteoglossum bicirrhosum Vandelli

(Text-fig. 1B)

Protractor hyoideus: is a stout muscle, unpaired except posteriorly over its origins (on each ceratohyal and, in part, aponeurotically from the inferior hyohyoideus of each side). It inserts, through a very short tendinous portion, onto the anterior part of the dentary around the symphysis. This anterior section of the muscle is split, horizontally, by the passage of a stout, transversely aligned *anterior intermandibularis*; that part of the protractor lying above the intermandibularis is thicker.

There is no median longitudinal aponeurosis, but there is a distinct tendinous inscription running transversely at about the middle of the muscle.

Holmquist (1911) and, later, Edgeworth (1935, fig. 277) described the muscle as divided horizontally into a broader, dorsal, *interhyoideus* portion, and a narrower, ventral (and medial) *posterior intermandibularis* portion; both authors also figure the transverse inscription. Despite careful dissection and probing, I could not find any such horizontal division in the muscle. Indeed, in the two specimens I dissected (28·6 and 34·0 cm standard length) the muscle could better be interpreted as being transversely and vertically divided. For example, that section lying anterior to the inscription is innervated by a branch of the mandibular V nerve, but most of the muscle behind the inscription is supplied by a branch of the hyohyoideus VII. This would seem to imply that the anterior part is derived from the posterior intermandibularis, and the posterior part from the interhyoideus However, since the inscription does not penetrate deeply into the muscle (*i.e.* it is not a complete, plate-like aponeurosis) and because the branch of the trigeminal nerve extends behind it, I would not be prepared to delimit the component parts on adult morphology alone. My uncertainty is reinforced by the condition of the muscle in *Pantodon buchholzi* (see page 16), where it seems to approach closely the condition described by Holmquist for *Osteoglossum bicirrhosum*.

Hyohyoideus. The superior portion (between the branchiostegal rays) is moderately developed. The inferior portion, although narrow, is fully muscular. It originates entirely from the first branchiostegal ray and has a tendinous insertion mainly onto the hypohyal of the opposite side; a few fibres, however, have a tendinous insertion onto the hypohyal of their own side. (It may be noted that Holmquist [1911, fig. 11] shows the right inferior hyohyoideus overlapping the left, but in all specimens I have examined [and in all other osteoglossids] left overlaps right).

Sternohyoideus (text-fig. 5). The greater part of this muscle originates on the dorsal surface of the horizontal limb of the cleithrum; a small part stems from the anterior tip of the conjoined cleithra. The sternohyoideus inserts onto the urohyal, but that part passing below the first gill arch is closely attached to the hypobranchial

by a thick connective tissue fascia. The muscle is also closely attached to the inner aspect of the ventrally directed bony processes on the second hypobranchials; each process is, however, entirely superficial to the muscle.

Ventral gill arch muscles (text-fig. 5). *Obliqui* muscles (linking cerato- and hypobranchial elements) are present on the first three gill arches. A small *rectus* muscle connects the fourth ceratohyal with the third hypobranchial.

No *rectus communis* is developed.

The proximal ends of the fourth and fifth ceratobranchials are joined, respectively, by the *anterior and posterior transversi*. The fifth ceratobranchial is also connected to the cleithrum by the strong external and internal *pharyngocleithrales*. The internal pharyngocleithralis is subdivided into a narrow posterior and a much broader anterior part. Both pharyngocleithrales have their origins medial to the sternohyoideus.

Scleropages leichardti Günther

(Text-fig. 1C)

In most details, the musculature of *S. leichardti* is identical with that described for *Osteoglossum bicirrhosum*. Comments made above on the morphology of the protractor hyoideus muscle and its components apply equally to the muscle in *Scleropages*.

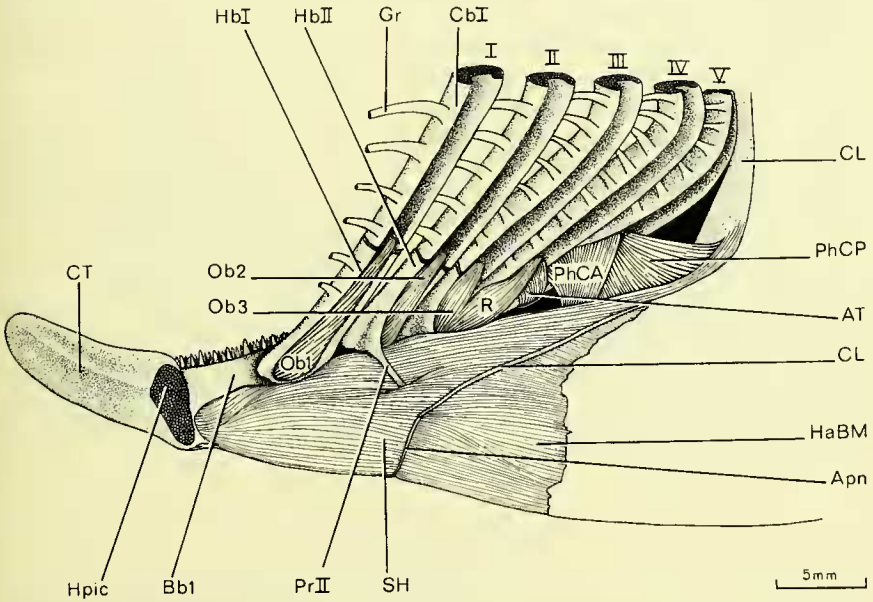


FIG. 5. *Scleropages leichardti*: ventral gill arch muscles and sternohyoideus in left lateral view. The hypohyal has been partly cut away.

Among the ventral gill arch muscles, the only intergeneric difference noted was that in *Scleropages* the proximal end of the rectus muscle is fused with the hypobranchial head of the obliquus of the third arch (text-fig. 5).

Subfamily **HETEROTINAE** (Nelson, 1968)

Heterotis niloticus (Cuvier)

(Text-fig. 1D)

Protractor hyoideus. This stout muscle originates on the ceratohyal and lower three branchiostegal rays of each side, but is a single element over its anterior half. It inserts directly, through short left and right heads, on either side of the dentary symphysis. Slightly anterior to the point of fusion between left and right halves, there is a very distinct transverse inscription; no other division of the muscle can be detected by dissection. The anterior part of the protractor is supplied by a branch of the mandibular V nerve, the posterior part by a branch of the hyohyoideus VII. The latter branch emerges from the medial side of the branchiostegal membrane at the base of the first ray; the main nerve continues forward, and supplies the inferior hyohyoideus muscle.

Heterotis is unusual in having a strong connective tissue link between the protractor hyoideus and the hypohyals (at a point near the union of the protractor's two halves).

A small and narrow *anterior intermandibularis* lies dorsal to the protractor hyoideus and does not pass through any part of it (*cf. Osteoglossum* and *Scleropages*).

Sternohyoideus. This stout muscle originates almost entirely from the dorsal surface of the horizontal limb of the cleithrum; a few ventral fibres stem from the anterior tip of that bone. It inserts onto the urohyal but is also firmly attached to the hypobranchial of the second arch and, less intimately, to the first hypobranchial as well. The ventral processes from the second hypobranchials are partly buried in the sternohyoid.

Ventral gill arch muscles. The most outstanding feature of these muscles is the development of a *rectus communis* from the fourth ceratobranchial to the base of the process on the second hypobranchial; there is also a tendinous connection between this muscle and the third hypobranchial.

In all other respects the gill arch muscles (including the *rectus*) are like those of *Osteoglossum* and *Scleropages*. The *pharyngocleithrales* of *Heterotis*, however, are simpler since the internal muscle is undivided.

Arapaima gigas (Schinz)

(Text-fig. 1E)

Protractor hyoideus: is a short, largely paired muscle originating from the ceratohyal and the basal parts of the second and third branchiostegal rays. Only about

the anterior third of the muscle is unpaired, the two halves meeting along a weak aponeurosis. Slightly anterior to this junction there is a transverse tendinous inscription.

The protractor inserts, through left and right musculose heads, on either side of the dentary symphysis. A small and narrow *anterior intermandibularis* passes through the muscle a little posterior to its insertion.

It is impossible, by inspection or dissection, to determine the extent of the protractor's component muscles, nor is it possible to determine the manner of their fusion.

Hyohyoideus. The superficial part is moderately well-developed and largely muscular. The inferior division is short and relatively stout; it inserts through a long tendon onto the hypohyal of the opposite side.

Sternohyoideus. Undoubtedly the sternohyoideus is the most characteristic muscle of *Arapaima gigas* (see text-fig. 6). It is divided, horizontally, into a small anterior and dorsal division, and a much larger unpaired ventral part. The latter originates (as is usual) on the horizontal limb of the cleithrum, and inserts on either side of the peculiarly shaped urohyal. In cross-section, this bone is shaped like an inverted T, with the arms extended to such a degree that the anterior half of the lower sternohyoid is completely covered by bone. A broad ligament from either side of the urohyal attaches it, ventrally, to the ceratohyals and hypohyals. The small ventral process of the second hypohyal barely contacts the dorsal part of this ventral sternohyoid division. Indeed, the process in *Arapaima* is the shortest found in any osteoglossid, and has the least intimate contact with the sternohyoid.

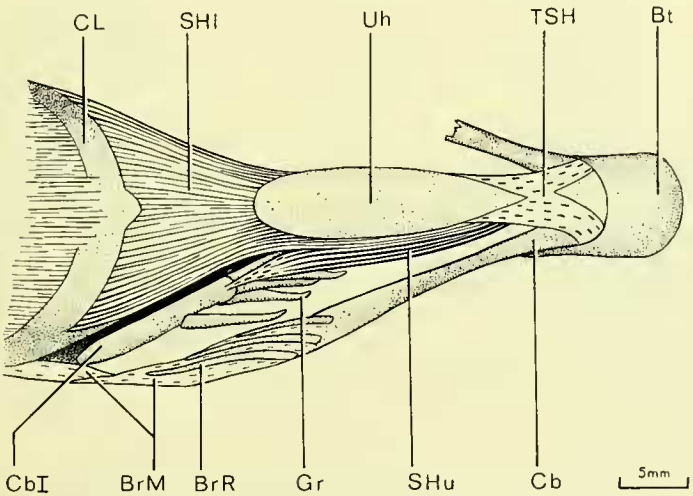


FIG. 6. *Arapaima gigas*: ventral view of the sternohyoid, to show its upper and lower divisions and their relationship with the urohyal, cleithrum and first hypobranchial. Semi-schematic; the lower jaw is not depicted. Cb=ceratohyal.

The dorsal division of the sternohyoid is paired. Each half originates on the ventral face of the first hypobranchial, and extends over almost the entire length of that bone (thus underlying the first obliquus muscle). The left and right halves meet, aponeurotically, in the midline; the broad tendon originating at this union inserts, somewhat asymmetrically, on the inner aspect of the ceratohyals near their tips. Although some part of the tendon inserts on the right ceratohyal, by far the greater part is attached to the left bone.

No other osteoglossid shows such clear-cut subdivision of the sternohyoid, or such asymmetry in its insertion. In fact, insertion of even part of the sternohyoid onto the ceratohyals is most unusual in teleosts. Nevertheless, it is difficult to identify the upper division of this muscle in *Arapaima* as other than part of the sternohyoideus. That other osteoglossids have a close association of the sternohyoid with the first and second hypobranchials, and that there is an incipient division of the muscle in *Heterotis* (see p. 14), all seem to support the recognition of a divided sternohyoid in *Arapaima*.

Ventral gill arch muscles: in *Arapaima* have the typical osteoglossid pattern; there is no *rectus communis*.

Obliqui are present on the first three arches; the obliquus of the third arch is closely associated with the well-developed *rectus* running almost in the midline from the fourth ceratobranchial to the third hypobranchial. Anterior and posterior *transversi* are present, as are stout and undivided internal and external *pharyngocleithralcs*.

Family **PANTODONTIDAE**

Pantodon buchholzi Peters

(Text-fig. 1F)

Protractor hyoideus (text-fig. 7): is a single muscle over its anterior half, but is paired posteriorly, with the left and right halves originating on the ceratohyal and lower three branchiostegal rays of their side.

The muscle is marked by a transverse inscription at the point where the two halves unite. At this point, the unpaired portion is visibly separable into a broad dorsal section (inserting on either side of the dentary symphysis) and a much narrower, more compact, median and ventral part which inserts, tendinously, onto the symphysis itself. Slight pressure with a probe along the horizontal sulcus demarcating the two parts separates them back to the level of the transverse inscription. Beyond this point there is considerable interchange between the parts, and the sulcus itself is no longer distinct.

A well-developed, stout, transverse *anterior intermandibularis* lies between, and separates, the dorsal and ventral parts of the protractor anteriorly.

In many respects, the condition of the protractor hyoideus in *Pantodon* resembles that described for *Osteoglossum* by Holmquist (*op. cit.*) and Edgeworth (1935); it will be recalled that I found a rather different arrangement in that genus (see p. 12).

Pantodon differs from Holmquist's description of *Osteoglossum* in that the muscles cannot be separated posteriorly beyond the transverse inscription. Holmquist and Edgeworth identify the entire length of the median, ventral section of the muscle in *Osteoglossum* as a protractor hyoideus (*i.e.* a posterior intermandibu aris in the terminology used here), and the overlying, broader part as the interhyoideus component.

Identifying the components of the protractor hyoideus in *Pantodon* is not easy, particularly since the innervation cannot readily be traced within the muscle. Judging from the position of the upper and lower insertions, and from the fact that the ventromedial segment is so clearly circumscribed, I would identify it as the posterior intermandibularis; the much larger muscle above, lateral to and behind it would then be the interhyoideus portion. In other words, a situation like that in the protractor hyoideus of *Salmo salar* (see Holmquist, 1911, and Dietz, 1912).

Hyohyoideus. Both the superior and inferior divisions are well-developed, the latter originating on the first branchiostegal ray, and inserting tendinously on the hypohyal of the opposite side.

Sternohyoideus. The lower third of this muscle originates on a broad aponeurosis with the ventral body musculature; the remainder stems from the dorsal surface of the horizontal limb of the cleithrum. Anteriorly, the sternohyoid inserts around the small urohyal which is completely embedded in the muscle. The medial face of

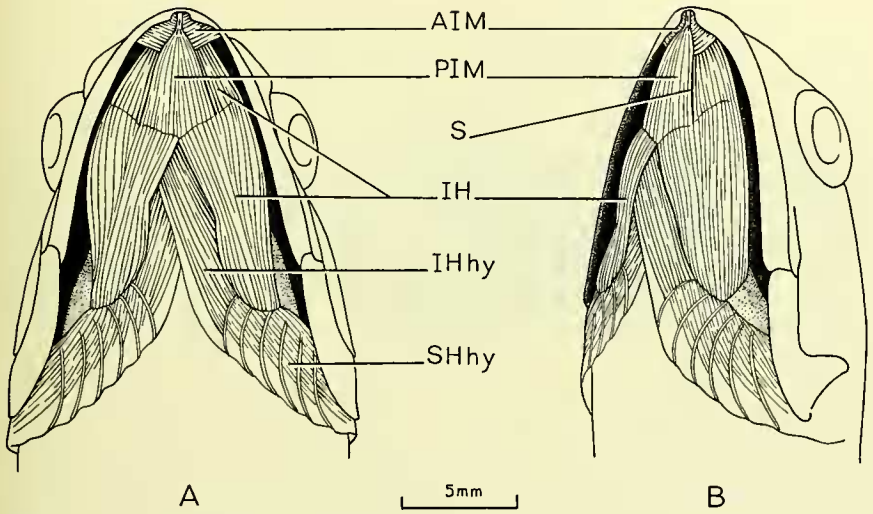


FIG. 7. *Pantodon buchholzi*: ventral hyoid musculature. A. In ventral view. B. In oblique ventro-lateral view. The transverse inscription (aponeurosis) is shown, but not labelled, in both views.

each process from the second hypobranchial is firmly but superficially attached to the sternohyoid, which is also closely attached by connective tissue to the ventral side of the first hypobranchial.

Ventral gill arch muscles. As in *Heterotis* (but not other osteoglossids) a distinct *rectus communis* is present; the small *rectus* from the fourth ceratobranchial to the third hypobranchial is distinct from the rectus communis but is closely applied to it. *Obliqui* are present on the first three arches; anterior and posterior *transversi* are well developed, and the pharyngocleithrales are simple but relatively stout.

Family **NOTOPTERIDAE**

Munshi has given a detailed description of the cranial muscles in the Asiatic species *Notopterus chitala*, and Nelson (1969) has listed the branchial muscles of the same species. In view of this previous work, I have concentrated on the two African species, *Papyrocranus afer* and *Xenomystus nigri* (see also Greenwood, 1963 and Nelson *op. cit.*). Some comments on Munshi's description of the hyoid muscles in *N. chitala*, and a general comparison of the hyoid and gill musculature in the three genera follow the separate accounts for *Papyrocranus* and *Xenomystus*.

Papyrocranus afer (Günther)

(Text-fig. 1G)

Ventral hyoid musculature (text-fig. 8). The most superficial (*i.e.* ventral) muscle has its origin, on each side, equally from the ceratohyal and from the basal part of branchiostegal rays 2 to 6. The two halves of this muscle join to form a single element over about the anterior half of their length.

Anteriorly, the muscle inserts onto the dentary through dorsal and ventral heads; the single, narrow and tendinous ventral insertion is onto the symphysis, while the broader, more musculose dorsal insertion is double and lies on either side of the symphysis.

This ventral muscle is innervated solely by a branch of the mandibular V nerve. Careful dissection shows that no branch of the hyohyoideus VII runs to it (see below under *interhyoideus*).

With respect to its innervation, the muscle differs from the topographically similar muscle (the protractor hyoideus) in osteoglossid and pantodontid fishes. Munshi (*op. cit.*) identifies the muscle in *Notopterus* as a *posterior intermandibularis* and I would agree with his identification, both on the grounds of the muscle's innervation solely from the trigeminal nerve, and because distinct interhyoideus muscles (innervated from the facialis nerve) are also present. It will be recalled

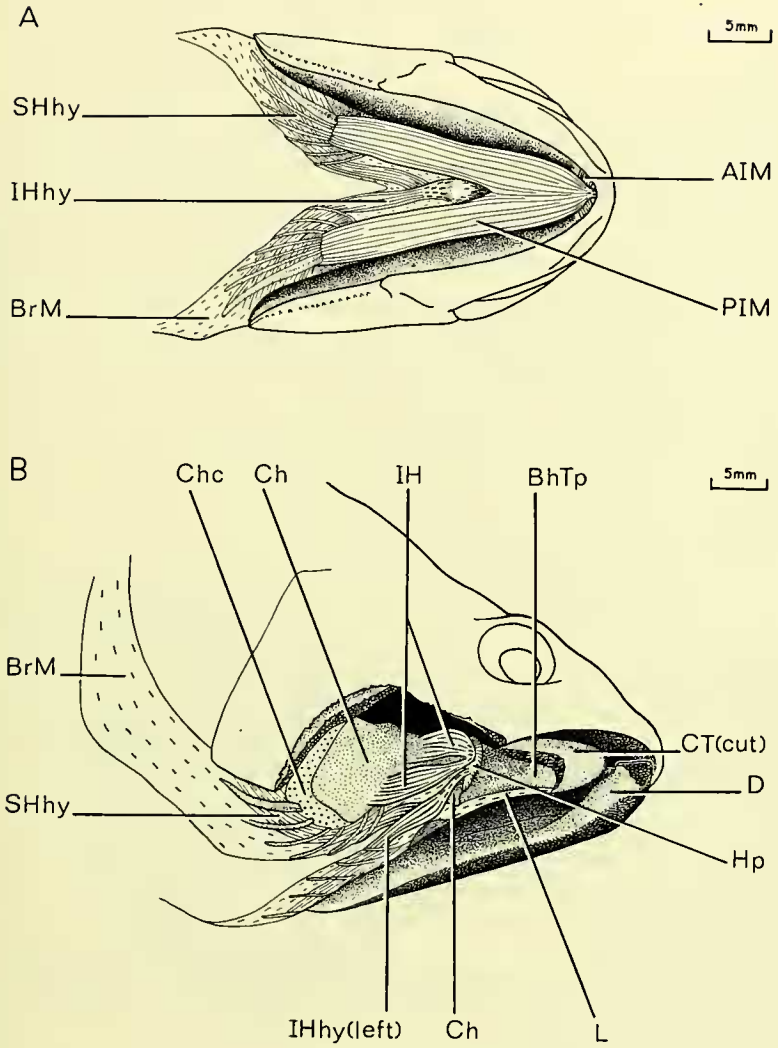


FIG. 8. *Papyrocranus afer*: A. ventral hyoid muscles, after removal of the skin. B. ventro-lateral view of head to show the interhyoideus muscles. The right half of the lower jaw removed, as is the cheek and jaw musculature of that side.

that in osteoglossoids the protractor hyoideus has a double (trigeminal and facialis) innervation, and that in these fishes no separate interhyoideus is present.

A small and weak *anterior intermandibularis* muscle lies between the dorsal and ventral insertions of the posterior intermandibularis. Its fibres are transversely orientated, and attach to the median face of the dentary on either side of the symphysis.

Interhyoideus (text-fig. 8). This paired muscle appears to be further divided on each side into a shallow lower portion, and a deeper upper part (see fig. 8B). Anteriorly, however, the two parts have a common tendinous insertion onto the dorsal surface of the hypohyal of the same side. The upper division originates entirely from the ceratohyal, but the lower part originates from the ventral margin of the ceratohyal and, in minor part, from the heads of the first two branchiostega. rays. The interhyoideus is innervated by a branch of the hyohyoideus VII nervel This nerve enters the lower muscle division after emerging from behind the branchiostegal rays and passing along the upper margin of the first ray.

Hyohyoideus. The superior division is rather poorly developed, and is almost completely tendinous. The inferior part is also tendinous but has its medial third strongly muscular (fig. 8B). This muscular section originates from the distal third of the first branchiostegal ray. The whole inferior hyohyoid inserts, tendinously, on the hypohyal of the opposite side (the left muscle passing ventral to the right).

Sternohyoideus (text-fig. 9). The large sternohyoideus originates entirely from the dorsal surface of the horizontal limb of the cleithrum. Ventrally, part of the muscle inserts, through a pair of tendons, onto the hypohyals and the anteroventral tip of each ceratohyal (a most unusual arrangement; see also *Arapaima*, page 15). However, the bulk of the sternohyoid inserts onto and around the small urohyal which is completely embedded in the muscle. (It should be noted that a pair of strong ligaments from the ventral face of the basihyal tooth-plate also attach to the urohyal and are, in consequence, partly covered by the sternohyoid.)

The median face and posterior margin of each ventral process (tendon bones) from the second basibranchial are firmly but superficially attached to the lateral face of the sternohyoid on each side. Anterior to this point the muscle closely approaches the first basibranchial but is not attached to it.

Ventral gill arch muscles (text-fig. 9) Well-developed *obliqui* are present on the first three gill arches; the muscles of all three arches insert on the respective ceratobranchial, but those on the first and second arch have a double origin, from the hypo- and basibranchial.

A distinct *rectus* runs from the third hypobranchial to the ceratobranchial of the fourth arch where it comes into close contact with the head of a stout *rectus communis* connecting that arch with the base of the ventral process (tendon bone) articulating with the second basibranchial.

The prox mal ends of the fourth and fifth ceratobranchials are joined, respectively, by the broad *anterior* and *posterior transversi*.

The external and internal *pharyngocleithrales* are well-developed, simple muscles whose origins lie medial to the sternohyoideus.

Xenomystus nigri (Günther)

(Text-fig. 1H)

In all major details the musculature of this species is like that of *Papyrocranus afer*. The most noticeable differences may be listed briefly.

Posterior intermandibularis. The origin is mainly from the ceratohyal, with only about one quarter stemming from the first branchiostegal ray. It inserts through a single broad head, an arrangement possibly correlated with the much weaker and rather ill-defined *anterior intermanibularis* in this species. As in *Papyrocranus* the posterior and anterior intermandibulares are innervated by a branch of the mandibular V nerve.

Hyohyoideus. The inferior divisions fuse in the midline before inserting onto the hypohyals.

Interhyoideus: in this species is a pair of undivided muscles fused anteroventrally, and inserting onto the hypohyals through a short tendon which wraps around the face of these bones.

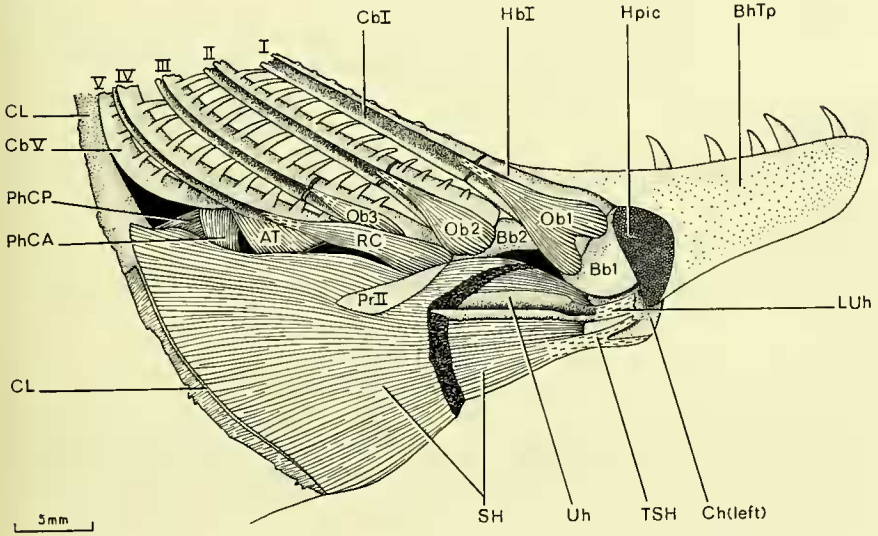


FIG. 9. *Papyrocranus afer*: lateral view of gill arch muscles and sternohyoideus. The anterior part of the sternohyoid has been dissected away on the right side to show the embedded urohyal. The tendon (TSH) inserts onto the right ceratohyal (removed) and right hypohyal (partly removed).

Gill arch muscles. I was unable to locate a separate *rectus* in *Xenomystus.* The *rectus communis* is present and large; like the *obliqui* it appears to be relatively larger in this genus. As in *Papyrocranus,* the obliqui of the first two arches originate from both the hypo- and the basibranchials.

PAPYROCRANUS AND *XENOMYSTUS* COMPARED WITH *NOTOPTERUS*

Basically, the musculature in the three genera is very similar (see Munshi, 1960 for *Notopterus*). In the two *Notopterus* species I examined (*N. chitala* and *N. kapirat*), the interhyoideus of each side is undivided (*i.e.* like that of *Xenomystus*); in *N. kapirat* it is indistinguishable ventrally from the upper, anterior part of the inferior hyohyoideus. According to Munshi (*op. cit.*) the left and right interhyoidei of *N. chitala* fuse medially. But, in his figure the muscles are shown as fan-like, horizontally disposed structures continuous with the inferior hyohyoidei, and running obliquely towards the midline; here the posterior portion of the left interhyoideus overlaps that of the right muscle. In the single specimen I dissected, the interhyoidei are vertically aligned (as in the other species considered), insert separately and are quite distinct from the inferior hyohyoidei. In other words, a situation identical with that found in *Papyrocranus.*

I would contest Munshi's identification of the muscle running from each basibranchial process (tendon bone) to the urohyal. This he calls the pharyngohyoideus (= rectus communis in the nomenclature used above). However, the figure shows the muscle as only partly distinct from the sternohyoideus (Munshi's rectus cervicus) below it, and no fibres are shown connecting with the upper posterior face of the tendon bones (as do those of the rectus communis). In the specimen I have examined (as in *N. kapirat, Papyrocranus* and *Xenomystus* also) it is not possible to separate the fibres attached to the tendon bone from those of the underlying sternohyoid. In contrast, the muscle I have identified as a rectus communis is distinguishable from the sternohyoideus even at its insertion onto the tendon bone where the two muscles are closely apposed. Thus it seems likely that the muscle Munshi identifies as a rectus communis is, in fact, part of the sternohyoideus.

Family **MORMYRIDAE**

The bauplan of the hyoid and gill arch musculature is remarkably constant in the Mormyridae, despite the great range of variation in head shape and jaw form of these fishes. The more outstanding features of the mormyrid musculature may be summarized as follows:—

(i) The muscles of the *protractor hyoideus complex* show the greatest degree of individuality and subdivision of any osteoglossomorph fishes; the interhyoideus muscles are enlarged and insert onto the lower jaw.

(ii) There is considerable hypertrophy of the *hyohyoideus* with the consequent loss of distinct superior and inferior divisions; the left and right halves of the muscle

join medially and the muscle is attached to the interopercula and ceratohyals as well as to the urohyal. This specialized musculature is associated with the peculiar branchial specializations of all mormyrids. For example, there is no discrete and expandible branchiostegal membrane, the rays being buried in the hyohyoideus, and the whole mass covered by skin continuous with that of the body; in consequence, the opercluar aperture is greatly restricted and lies entirely above the branchiostegal rays.

(iii) In the ventral gill arch musculature the *obliqui* have extensive areas of attachment, and the weakly developed *pharyngocleithrales* lie external to the sternohyoideus. The anterior part of the *sternohyoideus* is closely associated with the corresponding ventral elements of the gill arches, although there is never a direct musculose or tendinous insertion onto these bones.

Surprisingly, little attention has been paid to the cephalic and branchial musculature of mormyroid fishes. Holmquist (1911), drawing on his investigation of the hyoid musculature in *Gymnarchus niloticus*, noted certain peculiarities, but he was unable to extend his observations because of lack of comparative material. Nelson (1969) briefly commented on the gill arch muscles in Mormyridae and compared these with those of other osteoglossomorphs. The most comprehensive treatment is that of Bishai (1967) on *Mormyrus caschive*. Unfortunately, the nomenclature used by this author makes direct comparison very difficult, and I suspect that his description of the gill arch musculature is erroneous in many respects (see below, page 28).

Since the bauplan of the hyoid and ventral gill arch muscles is so similar in all mormyrids, I shall give a detailed description for one species only; deviations from this pattern will be noted for the other species examined.

Mormyrus kannume Forsk.

(Text-fig. 2A)

The snout in this species is slender, moderately decurved, produced and tubular, with the mouth small and terminal.

Posterior intermandibularis (text-fig. 10A): is a fairly thick muscle with originates, aponeurotically, over the anterior part of the hyohyoideus, and directly from the interoperculum of each side. It inserts through two muscular heads on either side of the mental cartilage (that is, it does not attach directly to the dentary). At about its midpoint there is a faint, longitudinal aponeurosis which extends anteriorly; posterior to this point both halves of the muscle are contiguous medially throughout their lengths. The posterior intermandibularis is broad and extends laterally almost to the ventral margin of each dentary, to which it is attached by a connective tissue sheet.

Anterior intermandibularis (text-fig. 10B): lies immediately above the posterior division. It is a relatively thin but expansive muscle extending longitudinally from the level of the posterior interopercular margin to a little behind the mental cartilage.

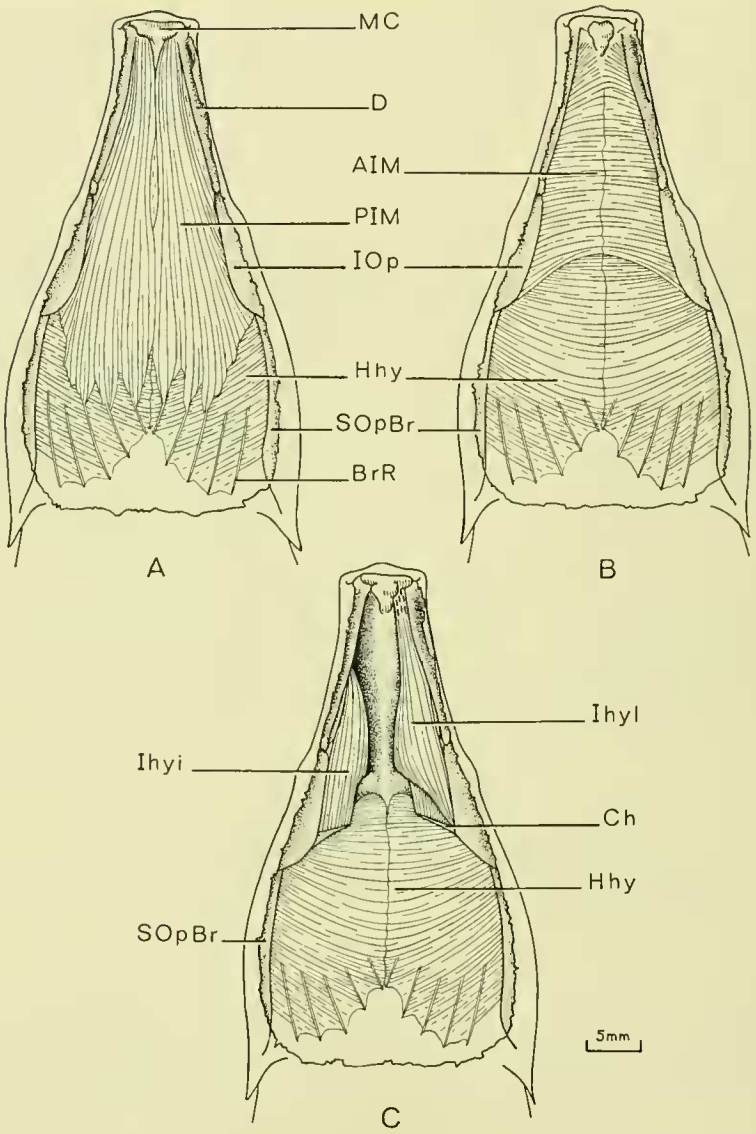


FIG. 10. *Mormyrus kannume*: ventral hyoid muscles. A. After removal of the skin. B. Posterior intermandibularis removed. C. Anterior intermandibularis removed; right lateral division of the interhyoideus muscle removed.

Laterally it inserts, directly, onto the interoperculum, articular and the dentary. All its fibres are transversely arranged; there is a faint but distinct median aponeurosis extending along the entire length of the muscle.

Both the anterior and posterior intermandibularis are innervated by a branch of the mandibular V nerve.

Interhyoideus (text-fig. 10C). A bilaterally paired muscle originating on the hyoid arch but inserting on the medial face of each dentary and articular, is identified as the interhyoideus because of its origin (the epi- and ceratohyal) and because of its innervation (a branch of the hyohyoideus VII).

The lateral (*i.e.* outer) muscle of each pair is the larger; it has a narrow origin from the upper part of the ceratohyal and part of the epihyal, and inserts tendinously onto the ventral margin of the dentary immediately lateral to the symphysis.

The inner and smaller muscle has a much wider origin (entirely from the ceratohyal) ventral to that of the lateral division. It inserts on the medial face of the dentary, and also the articular, considerably behind and above that of the outer division.

Hyohyoideus (text-fig. 10): is a stout, thick muscle with the left and right halves meeting medially along a fine aponeurosis. The branchiostegal rays are almost completely embedded in muscle; it is impossible to recognize separate superior and inferior divisions. The posterior part of the hyohyoideus is attached to the subopercular branchiostegal rays,[1] the middle section to the interoperculum, and the forward part to the anterior face and ventral margin of the ceratohyal laterally; medially the muscle is attached to the urohyal. All these connections are musculose.

Externally, the hyohyoideus is covered by skin which is continuous with that of the body and lower surface of the jaw. In other words, there is no separate branchiostegal membrane. Internally, the medial face of the hyohyoideus is bound to the overlying ventral body musculature by an extensive connective tissue union.

Sternohyoideus: is a large muscle originating mainly from the dorsal face of the horizontal cleithrum, but with a small ventral portion continuous with the hypaxial body muscles. The sternohyoid inserts on the urohyal but its antero-dorsal section is closely associated, through a connective tissue fascia, with the second basibranchial. The ventral processes from the second hypobranchials are, proximally, embedded in the sternohyoid; distally they lie outside the muscle but closely attached to its lateral face.

Ventral gill arch musculature (text-fig. 11). Well-developed *obliqui* are present on the first three gill arches; all are broad muscles extending onto the ceratobranchial well beyond its articulation with the small hypobranchial. From the first obliquus there is a distinct postero-medially directed slip of muscle which inserts onto the second hypobranchial. From the second obliquus a similar slip runs to, and inserts on, the second basibranchial. The third obliquus links only the cerato- and hypobranchial of its arch.

[1] In mormyrids the upper two branchiostegal rays are blade-like bones which have lost their articulation with the hyoid arch. Instead, the two bones are firmly attached to one another, and the upper bone is immovably attached to the lower margin of the operculum. Together, these two rays form an apparently immovable pseudosuboperculum.

A moderately developed *rectus communis* extends between the fourth ceratobranchial and the proximal end of the ventral process from the second hypobranchial. The muscle is closely applied to, but distinct from, the dorsal margin of the sternohyoideus. A short, broad and nearly triangular muscle joins the fourth and fifth ceratobranchials near their proximal ends. I cannot be certain about the identity of this muscle. It could be a displaced obliquus of the fourth arch or, more likely, part of this obliquus since there is a large transversus associated with the arch (all this assuming that obliqui are, primitively, associated with each arch; see Nelson, 1967).

The *anterior transversus* is moderately broad; it links the ventral tips of the fourth ceratobranchials. The *posterior transversus* runs obliquely forward so that it has the shape of a V, the apex inserting on the cartilaginous block lying between the ventral tips of the third and fourth ceratobranchials (the fourth basibranchial of Nelson, 1968). The arms of the V are closely applied to the ventral surface of each ceratobranchial.

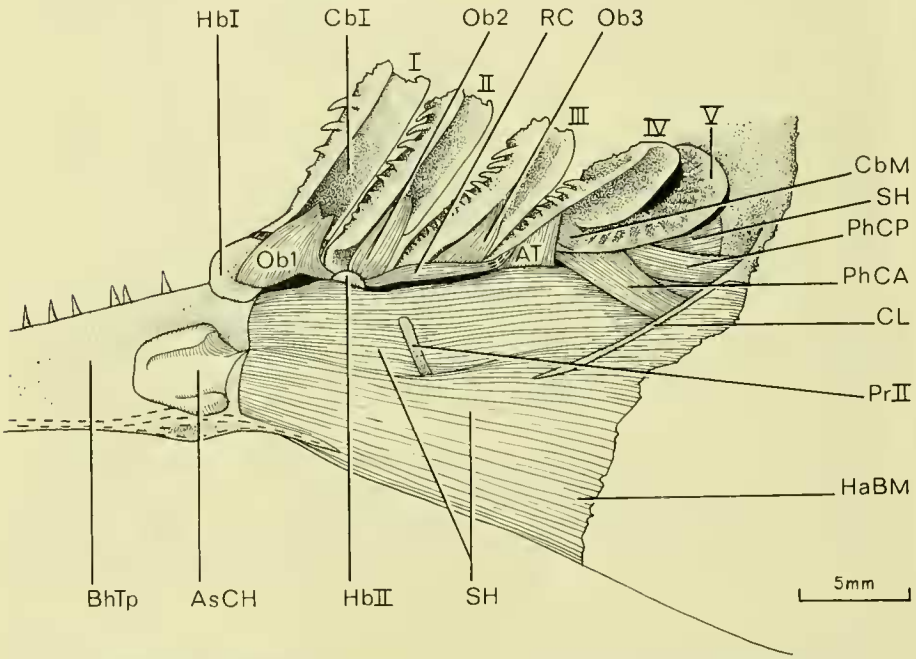


FIG. 11. *Mormyrus kannume*: ventral gill arch muscles and sternohyoideus in left lateral view. Not all the connective tissue surrounding the basihyal and urohyal has been dissected away.

External and internal *pharyngocleithrales* are present, but are not strongly developed. An unusual feature of these muscles in all mormyrids is their origin external to the sternohyoideus Both divisions, but especially the external one, have a deep and broad insertion on the fifth ceratobranchial.

Mormyrus caschive Linn.

(Text-fig. 2B)

Bishai i(1967) has given a detailed account of the cranial and branchial muscles in this species Unfortunately, I have been unable to dissect a specimen, but since in osteologcal and other features *M. caschive* is very similar to *M. kannume*, it seems reasonable to assume that the musculature would also be similar.

Thus, it is surprising to find a number of departures from the *M. kannume* condition in the ventral musculature of *M. cashive* as described by Bishai. Because muscle nomenclature used by this author differs from that usually employed, and because of the anatomical differences noted, I shall give a list of synonyms for the muscles involved and also comment on the apparent discrepancies between my observations on *M. kannume* and Bishai's on *M. caschive*.

In general, I would agree with Bishai's description of the superficial hyoid muscles. His *depressor labii inferioris* muscle is my posterior intermandibularis, and his *intermandibularis* is my anterior intermandibularis. The posterior intermandibularis of *M. caschive* (*cf.* text-fig. 10A with Bishai's fig. 4) is narrower anteriorly and seems to extend further posteriorly, covering the entire hyohyoideus (*i.e.* the *interbranchiostegalis* muscle of Bishai).

There is also substantial agreement in the arrangement of the deep ventral muscles (Bishai's *geniohyoideus internus* and *externus*, which are my inner and outer divisions of the interhyoideus). According to Bishai's figure 5, there are three divisions of this muscle, the innermost of which is not labelled. However, I suspect that the object which Bishai has labelled "geniohyoideus externus" is, in fact, a cut section of skin (or even cheek muscle); further, it seems that his "internus" muscle should be labelled "externus", and that the short unidentified innermost muscle is the internal division of his geniohyoid series (*i.e.* my interhyoid series).

The same figure also shows a condition of the sternohyoideus which I find difficult to accept. However, I think the figure is explicable when one considers Bishai's description of the ventral branchial muscles (*op. cit.*, page 21, and fig. 8). Here the author describes three large muscles, originating on each side from the cleithrum, and inserting on the urohyal and the ventral processes of the second hypobranchials. These muscles are identified by Bishai as "anterior portions of the pharyngoclavicularis muscle". Apart from an abuse of the term pharyngoclavicularis for muscles with these topographical relationships, it seems that Bishai failed to recognize their true identity as parts of the sternohyoideus (see page 25).

Bishai's *pharyngocleithralis posterior* apparently consists of both the external and internal divisions of this muscle.

I cannot find separate muscles in *M. kannume* corresponding to Bishai's *pharyngoarcualis anterior*, and *obliquus ventralis anterior* and *posterior* (of the first gill arch, see his fig. 8). Indeed, it seems that he has misinterpreted the double-headed condition of the first obliquus muscle which inserts, mainly, on the first hypobranchial but also has a slip passing to the second hypobranchial (see page 25).

Bishai does not describe a *rectus communis* muscle but his *fourth obliquus ventralis superioris* could well be part of a rectus communis (*viz.* that portion near its origin on the fourth arch and below the third arch).

Likewise, Bishai's *obliquus ventralis superioris* 5 seems to correspond to the small muscle, present in most mormyrids, which links the ceratobranchials of the fourth and fifth arches (see page 26).

The anterior transversus (*i.e.*, the *fourth transversus ventralis* of Bishai) requires no comment, but I believe that Bishai has misidentified the posterior transversus, and called it the *pharyngoarcualis posterior* (see page 51 for a discussion of the posterior transversus in mormyrids).

Mormyrus lacerda Casteln.

(Text-fig. 2C)

In this species the snout is relatively short, broad and but slightly decurved; the mouth is broad and terminal in position.

With few exceptions, the musculature is like that of *Mormyrus kannume*.

The *anterior intermandibularis* inserts onto the dentary and angular only; over its posterior third it fails to reach the lateral margins of the head. However, its posterolateral tips are attached to the ceratohyal near the origin of the interhyoideus.

The *posterior intermandibularis*, relative to that of *M. kannume*, is somewhat less substantial over its posterior half.

The *pharyngocleithrales* are complex. There are three distinct but contiguous heads on the cleithrum, all originating lateral to the sternohyoideus. At about the midpoint between girdle and ceratobranchial, the three separate muscles fuse, become tendinous and then, as a single element, become muscular again. Presumably this muscle should be considered as fused external and internal pharyngocleithrales.

Mormyrus hasselquisti Val.

(Text-fig. 2D)

In this species the snout is short, broad and but very slightly decurved. The mouth is broad and terminal.

The musculature of *M. hasselquisti* is virtually identical with that of *M. lacerda* (text-fig. 12). The anterior half of the *posterior intermandibularis* is, however, not quite so broad. It is separated from the ventral margin of the articular and dentary by a distinct connective tissue band through which the underlying anterior intermandibularis can be seen.

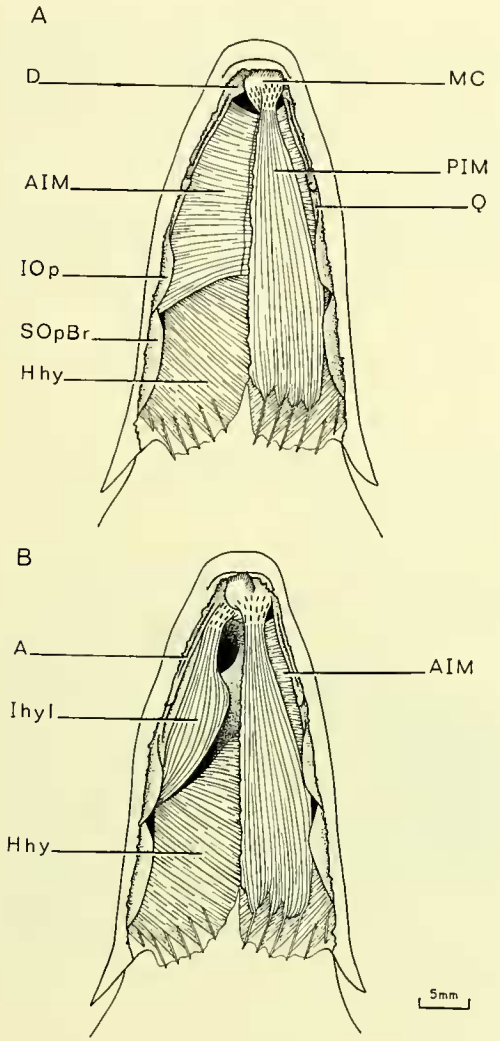


FIG. 12. *Mormyrus hasselquisti*: ventral hyoid muscles. A. Right half of posterior intermandibularis removed. B. Right half of the anterior intermandibularis removed.

Cyphomyrus discorhynchus (Peters)

(Text-fig. 2E)

The snout in this species is short, broad and strongly decurved, with the small mouth situated subterminally and its opening directed somewhat ventrally.

The genus *Cyphomyrus*, once part of the large and probably artificial assemblage of species in the genus *Marcusenius*, was separated out by Myers (1960).

There are several small but none the less characteristic features in the musculature of *C. discorhynchus*.

The *posterior intermandibularis* (text-fig. 13) is well developed, but anteriorly it does not extend to the lateral margins of the lower jaw. That section of the muscle originating on the interoperculum has its fibres more closely packed than are those in the larger section originating from an aponeurosis over the hyohyoideus muscle. The two parts of the intermandibularis can be separated easily by gentle traction.

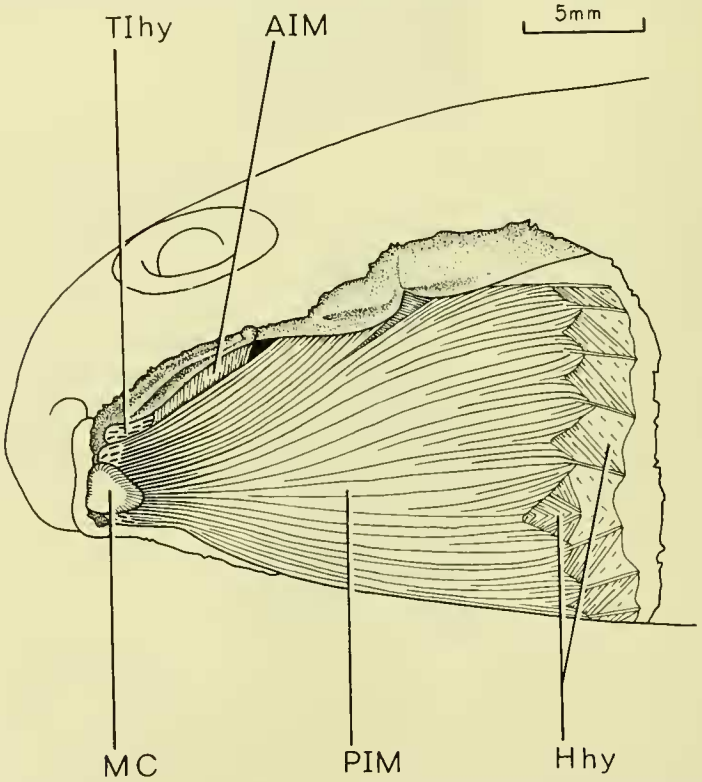


Fig. 13. *Cyphomyrus discorhynchus:* oblique ventro-lateral view of the hyoid musculature, after removal of the skin.

The *anterior intermandibularis* (text-fig. 13) is a short muscle showing some individual variability in length. In only one of the three fishes examined does this muscle extend anteriorly to the level of the posterior intermandibularis insertion; in one fish it extends posteriorly to the interoperculum (to which it is attached), in another it does not quite reach that point, whilst in the third fish, the muscle is attached to the interoperculum on one side but does not contact that bone on the other side. In all three specimens a slip from the posterior margin of the muscle passes upwards on each side to insert on the anterior face of the ceratohyal.

The major part of the *sternohyoideus* originates, aponeurotically, from the ventral body musculature; only a small part of the muscle originates from the cleithrum.

The ventral gill arch musculature is unusual in having, in addition to a *rectus communis*, a short but discrete muscle extending between the ventro-lateral ends of the second and third ceratobranchials.

Marcusenius cyprinoides (Linn.).

(Text-fig. 2F)

This species is usually classified in the genus *Gnathonemus*, but Taverne's (1968) recent investigations have shown that it and other short-snouted species are more properly included in the genus *Marcusenius* Gill as revised by Taverne (of which *M. cyprinoides* is the type species).

The snout of *M. cyprinoides* is relatively short and broad, and is not strongly decurved. The small mouth is terminal in position but has its opening directed somewhat dorsally. There is a noticeable submental protruberence into which the lower lip passes insensibly.

The *posterior intermandibularis* has the typical mormyrid origin from the interoperculum and from above the hyohyoideus. It inserts, however, entirely onto the enlarged submental cartilage; that is, it has no direct connection with the dentary.

The *anterior intermandibularis*, in contrast with that of the other species described above, is greatly reduced in size. Its length is only slightly greater than that of the eye, and it is confined to the articular region of the lower jaw. It inserts onto the articular of each side just before the articular-quadrate joint. The medial section of this muscle is tendinous.

The paired *interhyoideus* muscles, and the hypertrophied *hyohyoideus* are typical.

The *sternohyoideus* originates mainly from the dorsal surface of the horizontal limb of the cleithrum, but a small ventral part arises, aponeurotically, from the hypaxial body musculature. As in other mormyrid genera, the anterior part of the sternohyoid is closely associated with the ventral region of the first two gill arches. The ventral processes from the second hypobranchials are completely embedded in the sternohyoideus.

The *ventral gill arch muscles* are typical (see under *M. kannume*) except that there is, apparently, no short, triangular muscle connecting the fourth and fifth ceratobranchials.

Marcusenius victoriae (Worthington)

(Text-fig. 2G)

This species closely resembles *M. cyprinoides* (and like that species was formerly included in the genus *Gnathonemus*).

The musculature too is virtually identical with that of *M. cyprinoides*, although the *anterior intermandibularis* (text-fig. 14) is a little further reduced in size, and the muscle connecting the fourth and fifth ceratobranchials is present.

Gnathonemus longibarbis (Hilgendorf)

(Text-fig. 2H)

The snout is moderately short (especially as compared with other *Gnathonemus* species; see Taverne [1968]), the mouth small and terminal, and there is a long tubular submental barbel.

The *posterior intermandibularis* is an extensive muscle, originating, as is usual, over the hyohyoideus and from the interopercula. It has strong connective tissue attachments (in which some muscle fibres occur) to the ventral margin of the

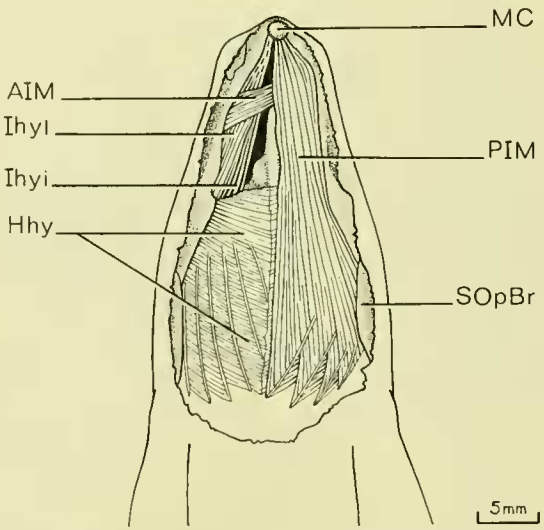


FIG. 14. *Marcusenius victoriae*: ventral hyoid musculature. The right half of the posterior intermandibularis muscle removed to show overlying muscles.

articular, dentary and preoperculum. Anteriorly, the muscle almost completely surrounds the massive, elongate submental cartilage, and reaches to its distal tip. A few fibres attach to the dentary at the base of the cartilage.

There is no trace of a distinct *anterior* (*i.e.* transverse) *intermandibularis*, nor can it be detected as a component of the posterior intermandibularis.

The *interhyoidei* are well developed but the bellies of the medial and lateral muscles on each side are not readily separated. Both divisions have distinct origins and insertions (like those in the species where the bodies of the muscles are distinct).

The *hyohyoideus* is typical (see page 25).

Most of the *sternohyoideus* originates on the cleithrum, but a small ventral portion is continuous with the hypaxial body musculature. As in other mormyrid species, the muscle has an intimate association with the ventral elements of the first two gill arches; the processes from the second hypobranchials are embedded proximally but lie on the surface of the sternohyoid distally.

The ventral gill arch muscles are typical (see page 25 *et seq.*).

Campylomormyrus elephas (Blgr.)

(Text-fig. 21)

Previously placed in the genus *Gnathonemus*, this species has, on osteological grounds, been reclassified, with others, in the genus *Campylomormyrus* (see Taverne, 1968).

The snout of *C. elephas* is greatly elongate, is tubular and strongly decurved; the tip lies well below the ventral head profile. The mouth is small and, relative to the snout, terminal. Because of the snout's decurvature the mouth opening is directed ventrally. The lower lip is continuous with a short, root-like mental barbel.

Posterior intermandibularis (text-fig. 15A and B): is a complex muscle, paired posteriorly, single anteriorly. The single portion extends from about the level of the quadrate-articular joint to the tip of the mental cartilage on which it is inserted. At no point along its length does this part of the muscle insert onto the dentary or articular.

The paired part is subdivided and has, on each side, several sites of origin. A little behind the point where the two halves of the muscle unite, each is divisible into more or less readily distinguishable dorsally and posterodorsally directed branches (text-fig. 15A). The area between these divisions is, however, traversed by a few interconnecting fibres. The dorsal branch is attached to the dentary and the articular while the posterodorsal branch is attached only to the interoperculum. The points of attachment should be considered as the sites of origin for the muscle as a whole.

Near the insertion of the posterodorsal branch (on the interoperculum) it is joined by a third division which originates, aponeurotically, over the hyohyoideus. This third branch, compared with the hinder part of the posterior intermandibularis in

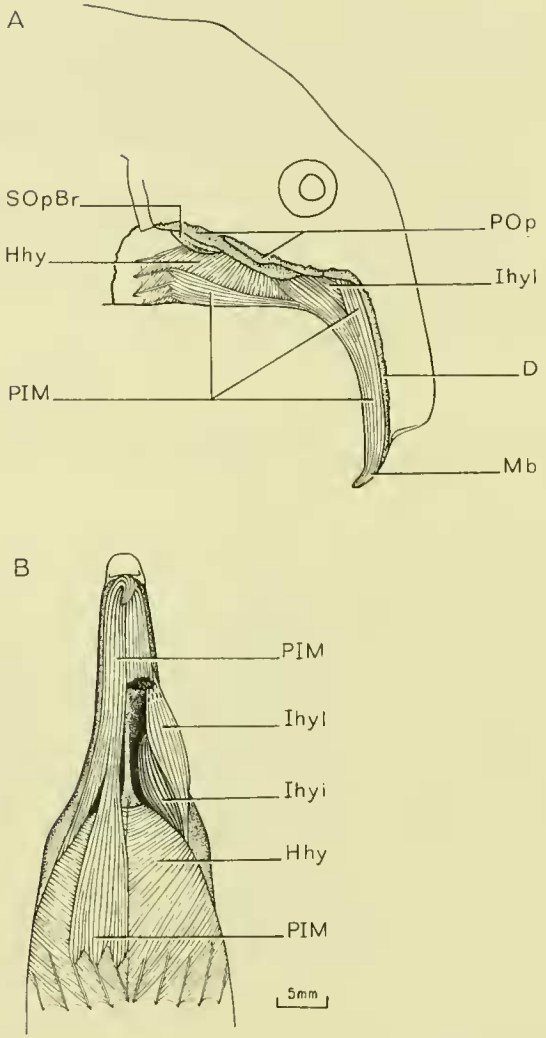


FIG. 15. *Campylomormyrus elephas*: A. Ventral hyoid muscles in lateral view after removal of the skin. B. The same, in ventral view, with the posterior three quarters of the left half of the posterior intermandibularis removed, and the left lateral division of the interhyoideus displaced laterally.

other mormyrids, is rather narrow and does not join its counterpart, although the two approach one another closely in the midline (see text-fig. 15A).

The *anterior intermandibularis* is, apparently, absent.

The *interhyoideus* (text-fig. 15B) like that of *Gnathonemus*, is incompletely subdivided (see page 33).

The *hyohyoideus* conforms with the typical pattern for mormyrids.

The *sternohyoideus* originates, about equally, from the cleithrum and the hypaxial body muscles. It inserts onto the urohyal and has close connections with the second basibranchial and other ventral elements of the first two gill arches. The processes from the second hypobranchials are embedded proximally; distally each lies superficially on, but attached to the sternohyoid flank.

The *ventral gill arch muscles* are typical (see page 25); the muscle linking the fourth and fifth ceratobranchials is present.

Petrocephalus bane (Lacép.)

(Text-fig. 2J)

The snout is short and broad, the mouth broad and subterminal, and lies almost immediately below the eye.

The text-figures for *P. catostoma* are, in general, applicable to this species as well.

Posterior intermandibularis. The two halves of this muscle are narrowly separated medially by a fine aponeurosis. The muscle originates from the first two branchiostegal rays and from above the hyohyoideus. It inserts, tendinously, along the entire ventral margin of the short lower jaw from symphysis to articular-quadrate joint. The uppermost fibres of this muscle separate easily from the ventral fibres, and in one specimen there appears to be some exchange of fibres between the posterior intermandibularis and the overlying interhyoideus muscle (see below). Close contact between these muscles is enhanced by the complete absence of an *anterior intermandibularis.*

Petrocephalus bane, unlike the species described before, has only one *interhyoideus* present on each side. The muscle, despite its great relative depth has a narrow origin on the dorsal part of the anterior face of the ceratohyal. In contrast, it has a deep and extensive insertion on the inner aspect of the dentary and articular, linearly from a point near the symphysis almost to the joint with the quadrate, and vertically from dorsal to ventral margins of these bones.

The *hyohyoideus* is well-developed and of the usual form, except that only a very small part is inserted onto the urohyal.

The *sternohyoideus* originates about equally on the cleithrum and from the hypaxial body muscles.

The *ventral gill arch muscles* are typical, with a small interceratobranchial muscle between the fourth and fifth arches (see page 25 *et seq.*).

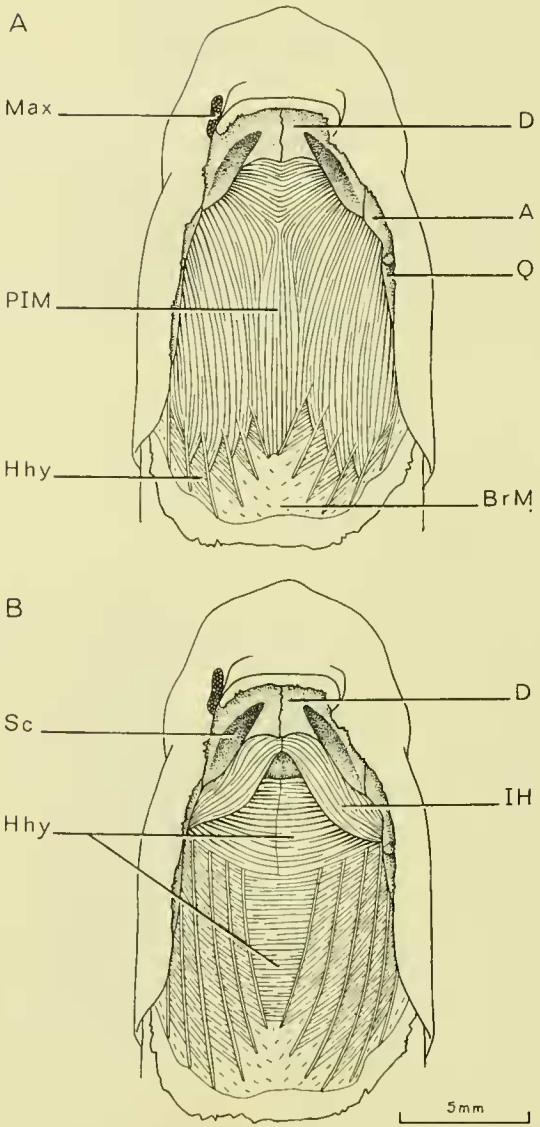


Fig. 16. *Petrocephalus catostoma*: ventral hyoid muscles. A. After removal of the skin. B. After removal of the posterior intermandibularis muscle.

Petrocephalus catostoma (Günther)

In its superficial morphology this species closely resembles *P. bane*; the myology is likewise very similar.

The *posterior intermandibularis* (text-fig. 16A) of *P. catostoma* has a more extensive origin over the hyohyoideus, and the tendinous part of the insertion is wider in this species. Some anterior fibres are almost transversely arranged (text-fig. 16A), thus contrasting with the obliquely orientated fibres posteriorly. Since no distinct *anterior intermandibularis* can be located in this species either, it is tempting to consider these transverse fibres as remnants of an anterior muscle now fused with the posterior part.

As in *P. bane*, only one interhyoideus (text-fig. 16B) is present on each side. These muscles are completely free from the underlying intermandibularis.

In all other respects the musculature of the two species can be considered identical, and typical of the family.

Isichthys henryi Gill

(Text-fig. 2K)

The broad snout of this species is relatively short and is not at all decurved. The mouth is terminal, horizontal and rather broad.

The *posterior intermandibularis* (text-fig. 17) of *I. henryi* shows very considerable reduction when compared with that muscle in all the species described above. The

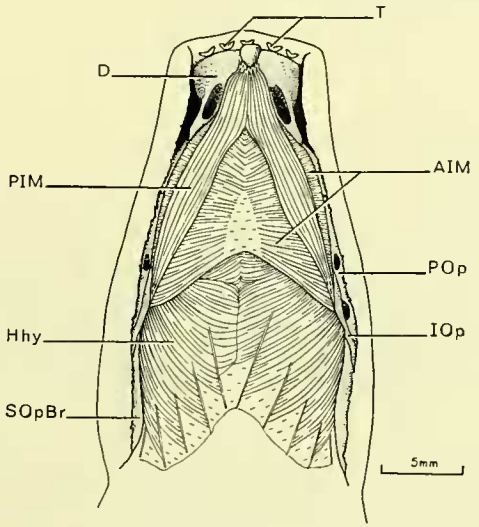


FIG. 17. *Isichthys henryi*: ventral hyoid muscles, after removal of the skin.

muscle is reduced to a narrow V-shaped band of fibres with the apex directed anteriorly; its origin is entirely from the interoperculum, and its tendinous insertion is onto the small mandibular cartilage lying above the interdentary symphysis.

Overlying the narrow posterior intermandibularis is the broad *anterior intermandibularis* (text-fig. 17) which extends across the lower jaw from the level of the posterior interopercular margin to immediately behind the interdentary symphysis. The muscle has a largely musculose insertion onto the ventral margins of the dentary and articular; its fibres are separated medially by a posteriorly broad but anteriorly narrow aponeurosis. Over the anterior quarter of the muscle the fibres are arranged almost transversely, but elsewhere they run obliquely forward.

The *hyohyoideus* (text-fig. 17) shows typical hypertrophy, and there are distinct lateral and medial *interhyoideus* muscles on each side.

The *sternohyoideus* originates about equally from the cleithrum and, aponeurotically, from the hypaxial body musculature. As usual, the sternohyoid is closely associated with the ventral elements of the first two gill arches. The ventral processes of the second hypobranchials lie superficial to the lateral surface of the sternohyoid, but are closely bound to it by connective tissue.

The *ventral gill arch musculature* conforms to the typical pattern (see page 25); the small muscle between the fourth and fifth ceratobranchials is not clearly differentiated and seems to be a slip from the *anterior transversus*. The *posterior transversus* is a narrow muscle but is otherwise typical.

Mormyrops anguilloides (Linn.)

(Text-fig. 2L)

The snout is relatively short in *M. anguilloides*, and is not decurved. The mouth is wide and terminal.

A specimen of the closely related *M. deliciosus* (Leach) was also dissected and its musculature found to be identical with that of *M. anguilloides*.

Posterior intermandibularis (text-fig. 18A). The muscle thought to be a posterior intermandibularis (see below) is a largely tendinous sheet within which lies a narrow band of transverse fibres arranged on either side of a median aponeurosis. Posteriorly, a short, upwardly directed slip of muscle runs to each interopercle; there is also a broader posterior extension of the muscular part which ends, aponeurotically, above the hyohyoideus (text-fig. 18A). Fibres in this part of the muscle are longitudinally orientated. The attachments to the interoperculum and the aponeurotic connection over the hyohyoideus should, presumably, be considered as the origins of the muscle; its insertion is directly onto the dentary near and on the symphysis (there being no mental cartilage in this species). The lateral and tendinous part of the muscle is attached to the interopercula, preopercula, the articulars and the dentaries.

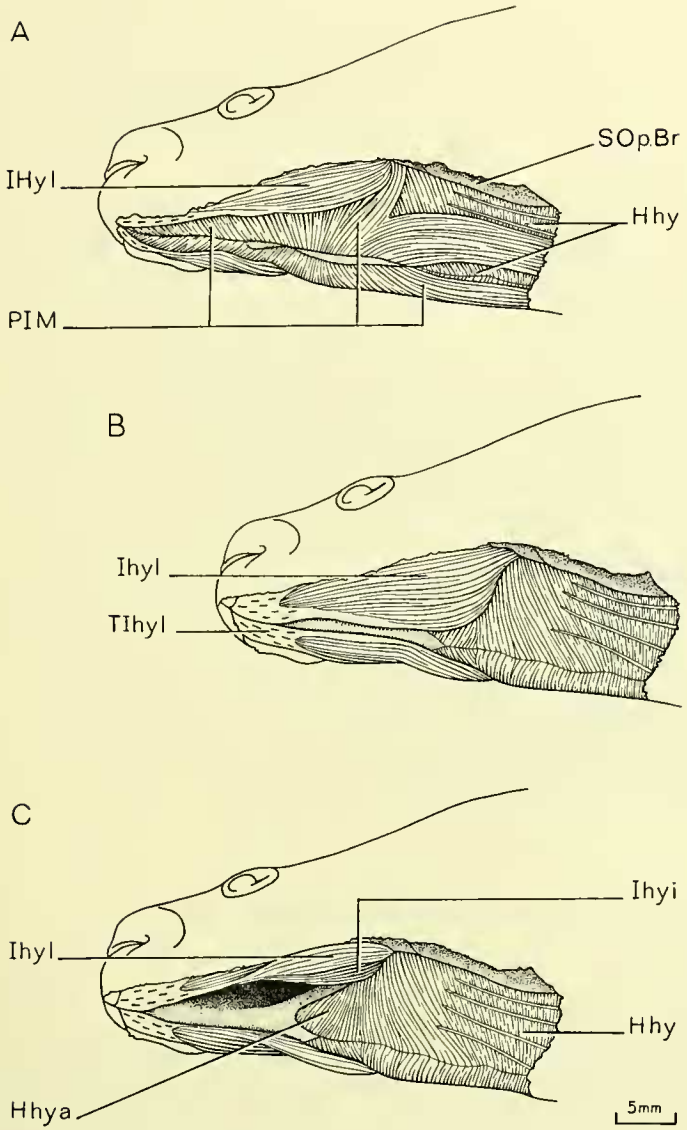


FIG. 18. *Mormyrops anguilloides*: oblique ventro-lateral view of the ventral hyoid muscles. A. After removal of skin. B. After removal of posterior intermandibularis muscle C. As in B but with lateral division of left interhyoideus reflected to show the inner division of that muscle.

No discrete *anterior intermandibularis* is present. The possibility of this muscle having fused with the posterior division cannot be overruled because the muscle thought to be the posterior intermandibularis is fairly clearly demarcated into an anterior part with transverse fibres, and a posterior sector with longitudinal fibres (see above). If the posterior and anterior intermandibulares are fused, then *Mormyrops* presents a rare condition among the mormyrids (but see also *Petrocephalus catostoma*).

The interhyoideus in *Mormyrops* also exhibits certain peculiarities (text-fig. 18B, C). As is usual, the lateral muscle of each pair is the larger. It originated dorsally on the anterior face of the ceratohyal, but it has two insertions, one directly onto the inner and ventral aspects of the dentary and articular, the other, tendinously, onto the anteroventral face of the dentary immediately lateral to the symphysis.

The smaller median muscle also originates on the anterior face of the ceratohyal but it inserts, aponeurotically, onto the median aspect of the lateral muscle. In other words, it has no direct attachment to the lower jaw. Indeed, the separation between the two muscles is very slight even near their origins and there is an exchange of fibres between them (a condition reminiscent of that in *Gnathonemus* and *Campylomormyrus* [see pages 33 and 35 respectively]).

The *hyohyoideus* (text-fig. 18) shows typical hypertrophy and relationships with other structures (see page 25).

Most of the *sternohyoideus* originates as an extension of the ventral body musculature; only a small part stems from the cleithrum. The processes from the second hypobranchials are fairly deeply embedded in muscle.

The *ventral gill arch muscles* are typical (see page 25), but the small muscle between the fourth and fifth ceratobranchials appears to be missing, and the slip from the first obliquus is greatly reduced in size.

The *pharyngocleithrales* are moderately well-developed, especially the external division.

Hyperopisus bebe (Lacép.)

(Text-fig. 2M)

The snout is relatively short and not decurved, the mouth moderately broad, terminal in position and horizontally directed.

Hyperopisus bebe is unique among mormyrids in having greatly enlarged and molariform teeth on the parasphenoid and apposing basibranchial tooth plate. Not only are the teeth enlarged, but they occupy a much broader area of attachment in both places than is usual among species with small conical teeth (see figs. in Taverne, 1968).

The *posterior intermandibularis* (text-fig. 19A) shows a degree of reduction comparable with that in *Isichthys*. From the interoperculum of each side a moderately

developed, strap-like muscle extends forward to insert on the small mental cartilage. Dorsally, the muscle has no contact with the ventral margin of the lower jaw. Between the arms of the strap-like muscle there is a broad tendinous sheet of tissue extending back to about the level of the posterior interopercular margin. Here it becomes continuous with the tendinous part of the overlying anterior intermandibularis. The margin of the tendon passes insensibly into a number of weak muscle-fibre bundles which, in turn have an aponeurotic connection with the hyohyoideus (see text-fig. 19A).

Immediately above the posterior intermandibularis is the well-defined and thick *anterior intermandibularis*. Except for a short distance posteriorly there is no median aponeurosis in this muscle, whose fibres extend from side to side of the lower jaw (text-fig. 19B). Insertion is onto the ventral margins of the dentary, articular, preoperculum and interoperculum, and, anteriorly, onto the mental cartilage. The anterior intermandibularis extends from the level of the vertical preopercular arm to a little behind the interdentary symphysis.

The *interhyoideus* muscles have a characteristic and complex form in *Hyperopisus* (text-fig. 19C–D). The ventro-lateral muscle of each pair is the smaller and is largely tendinous (see text-fig. 19C–D). It originates on the epihyal (with a very small part from the head of the fourth branchiostegal ray), and runs straight forward to insert on a low ventral process of the dentary.

The inner and dorsal muscle is divided, from near its origin, into two elements, one directed horizontally, the other (the innermost) running laterally and anteriorly (text-fig. 19C–D). The medial subdivision is the smaller of the two. It arises from some of the dorsal and external fibres of the lateral subdivision near the upper part of its origin. From a narrow beginning, the medial subdivision fans out so that it comes to extend along the ventral margin of the urohyal (anterior, that is, to the insertion of the hyohyoideus). The left and right medial subdivisions meet in a fairly narrow aponeurosis over the urohyal; some fibres from the underlying anterior intermandibularis also are attached to this tendinous tissue. Anteriorly, the aponeurosis is extended as a short tendon which inserts onto the dentary immediately below the symphysis.

The lateral subdivision of the inner interhyoideus has a broad origin from almost the entire anterior face of the ceratohyal. Its fibres run outwards and forwards, crossing above those of the outer division. The muscle inserts, either directly or through a narrow tendinous margin, onto the inner aspect of the quadrate, articular, and anteriorly, the dentary (text-fig. 19C–D).

The *hyohyoideus* (text-fig. 19C–D), although well-developed, gives the impression of being relatively less massive in this species. The anterior section is not as thick as in the other species described, and the interbranchiostegal portions are also weaker. As usual, the hyohyoideus inserts on the interoperculum, ceratohyal and urohyal, the latter insertion being relatively more extensive than in most of the other mormyrids examined.

The *sternohyoideus* is a short, deep muscle whose origin is entirely from the dorsal face of the cleithrum. The processes from the second hypobranchials curve out-

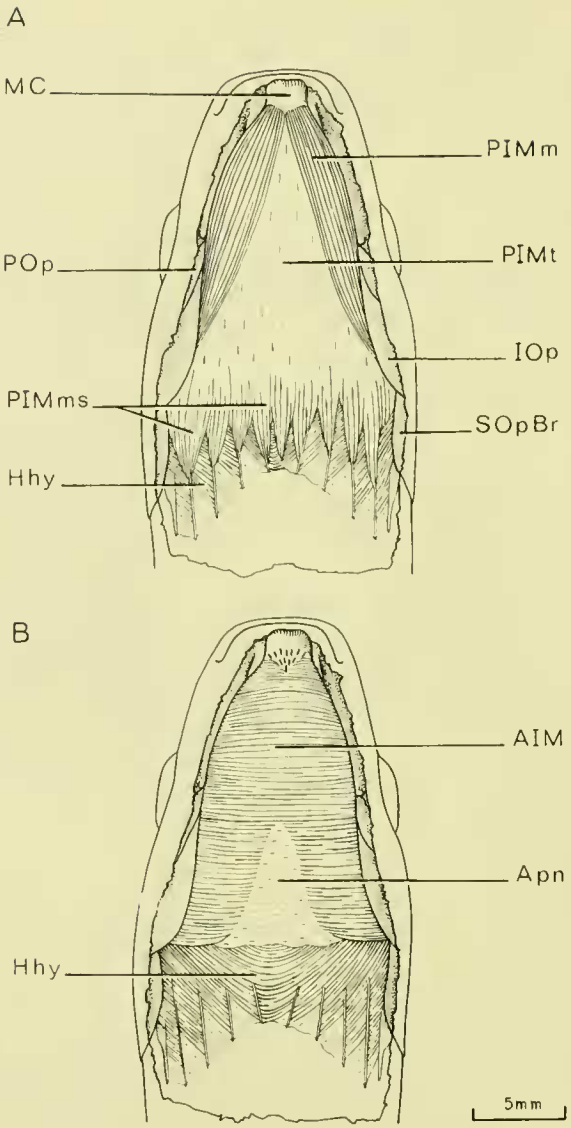
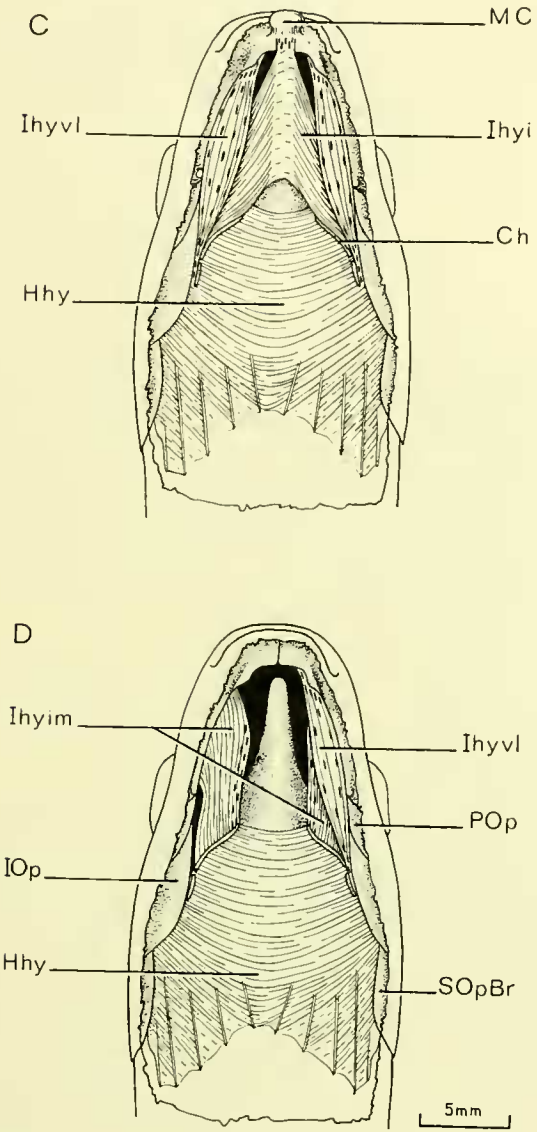


FIG. 19. *Hyperopisus bebe*: ventral hyoid muscles. A. After removal of skin. B. After removal of posterior intermandibularis muscle and tendon complex. C. After removal of anterior intermandibularis muscle. D. Right ventro-lateral division of the interhyoideus muscle removed to show underlying innermost division of this muscle complex. Entire inner (medial) division of this complex also removed.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wards and slightly backwards so as to lie almost horizontally; each lies superficial to the sternohyoid but is closely bound to that muscle.

The *ventral gill arch musculature* is like that of *Mormyrus* (see page 25), except that there is no muscle linking the fourth and fifth ceratobranchials. The external *pharyngocleithralis* has a short tendinous section at about the middle of its visible length, and the entire external division is virtually tendinous.

Family GYMNARCHIDAE

Gymnarchus niloticus Cuvier

(Text-fig. 2N)

The snout in *Gymnarchus niloticus* is relatively elongate, moderately broad and is not decurved. The terminal mouth is horizontally placed and its cleft extends much further posteriorly than in any mormyrid species. *Gymnarchus* is also unusual in having no teeth on the parasphenoid, and in lacking basibranchial tooth plates (see Nelson, 1968 and Taverne, 1970).

Holmquist (1911) has given a fairly detailed account of certain muscles; his description and figures were later used by Edgeworth (1935). Neither author was able to carry out comparative studies on other mormyroids and it is thus understandable how they came to emphasize the apparent similarities between *Gymnarchus* and *Albula*, in particular the hyperdevelopment of the transverse intermandibularis muscle.

Although these similarities do exist, and although *Gymnarchus* departs from the typical mormyrid condition, the similarities between it and *Albula* are less than those shared with the Mormyridae. In particular, one may note the shared specializations in the ventral gill arch musculature and the sternohyoideus.

The *hyoid musculature* (text-fig. 20). Immediately below the skin, and closely adherent to it, there is a broad, generally thick sheet of muscle which thins out posteriorly. It is attached to the operculum, sub- and interopercula, the preoperculum, dentary and articular. Anteriorly, this muscle inserts around the ventral margin of the mandibular arcade; posteriorly it extends to the level of the branchial opening (text-fig. 20). Throughout its length the fibres of the muscle are transversely arranged and extend from side to side without any indication of a median aponeurosis. Innervation is from a branch of the mandibular V nerve.

Holmquist (*op. cit.*) identifies this muscle as an intermandibularis; from the transverse arrangement of its fibres (text-fig. 20) it would seem to be homologous with the *anterior intermandibularis* of mormyrids. Since there is no trace of any muscle ventral to this sheet, and because there are no indications of longitudinal fibres in the sheet, one must conclude that a posterior intermandibularis is absent.

Immediately above the intermandibularis is a pair of muscles that insert, anteriorly, on the inner aspect of the dentary on either side of the symphysis (text-

fig. 20). Neither muscle meets the other at any point, although they are closely aligned anteriorly. The muscles originate in part from the epi- and ceratohyal, and in part from the first branchiostegal ray. In large individuals each muscle is incompletely divided, horizontally, so as to virtually form a small dorsal and larger ventral muscle (text-fig. 20). The ventral subdivision is that described above; the dorsal part originates on the epihyal and inserts on the inner face of the dentary about halfway along its length. The smallest fish examined (14·0 cm standard length) has no division, or even incipient division, in the muscle; consequently the single muscle on each side appears to have a double insertion, one anteriorly and the other laterally at about the middle of the dentary.

These muscles (or muscle) correspond, in most details, to the *interhyoideus* of mormyrids, and are identified as such in *Gymnarchus*.

One difference in the interhyoid of *Gymnarchus* is the considerable proportion of muscle originating from the first branchiostegal ray (text-fig. 20). In mormyrids the interhyoid originates exclusively from the hyoid bar, and there is complete separation between the interhyoid and the hyohyoideus. The situation in *Gymnarchus* is very different. In fact, the muscle described above could well be a combined inter- and hyohyoideus. In *Gymnarchus* the only clearly recognizable *hyohyoideus* is the superior or interbranchiostegal ray portion (text-fig. 20); here it is represented by a few, well-spaced oblique fibres running between the branchiostegal rays. No distinct inferior hyohyoid can be recognized. Indeed, those fibres, which, topo-

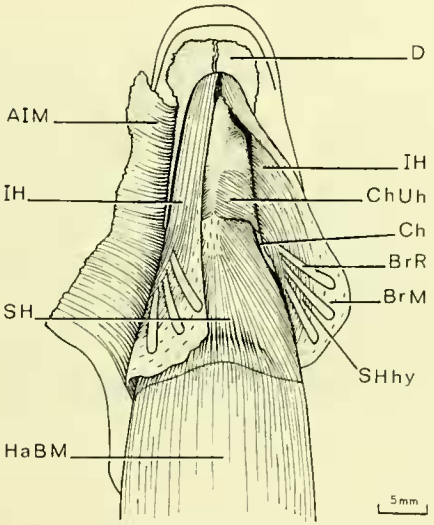

Fig. 20. *Gymnarchus niloticus*: ventral hyoid musculature. Anterior intermandibularis cut and reflected to the right; left interhyoideus reflected to the left.

graphically, would form the inferior hyohyoid merge with the fibres forming the body of the muscle I have identified as the interhyoideus. Thus, the situation in *Gymnarchus* has all the appearance of a secondary return to the primitive condition in which the constrictor hyoideus ventralis has not split into inter- and hyohyoid portions. That the condition is not strictly a primitive one is indicated by the separate left and right inter- cum-hyohyoideus muscles.

The poorly developed hyohyoideus of *Gymnarchus* contrasts markedly with the hypertrophy of that muscle in all mormyrids. *Gymnarchus* also differs in having the branchiostegal rays (and their associated musculature) free from the ventral body muscles. Nevertheless, the branchiostegal membrane (*i.e.* the interray muscles and tendons) still does not provide a ventrolateral floor to the branchial cavity. This is formed by a membranous sheet which runs, on each side, from the inner face of the corresponding ceratohyal to the upper part of the sternohyoid muscle. In effect, each branchiostegal membrane constitutes a lateral half pouch (opening medially but blind anteriorly) over the sternohyoid and hypaxial muscles. The intermandibularis muscle covers these pouches and their medial openings. This greater pouch is open posteriorly across the breadth of the body.

Identifying the hyoid muscles of *Gymnarchus* is further complicated by the presence of a pair of small muscles that lie immediately anterior to the sternohyoid

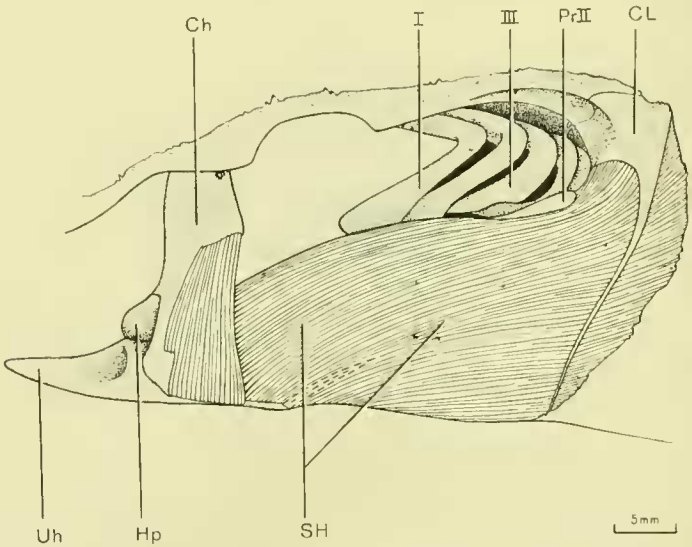

FIG. 21. *Gymnarchus niloticus*: Sternohyoid and ceratohyal-urohyal muscles in left lateral view; semi-schematic.

insertion (text-figs 20 & 21). Each muscle has its fibres arranged almost vertically, and is attached to the ventral margin of the ceratohyal above and to the urohyal below. It seems likely that these are the muscles which Holmquist (*op. cit.*) showed in his figure and which he tentatively identified as branchio-mandibulares (labelled:? genio-branchialis in Edgeworth's [1935] reproduction of Holmquist's figure). However, Holmquist does clearly state that the fibres run longitudinally.

Holmquist (*op. cit.*) commented that he had not seen such a muscle in any other teleosts, and neither have later workers described similar muscular arrangement.

Holmquist's and Edgeworth's identification of this muscle are tentative, but I have difficulty in understanding why they considered it to be a branchiomandibularis or geniobranchialis. Such a muscle is not found in teleosts, and morphologically it is one connecting the lower jaw with the hyobranchial skeleton. Be that as it may, the identification of the muscle pair still poses several questions. That each is attached to both the ceratobranchial and the urohyal suggests one of three things: that the muscle could be a subdivision of the interhyoideus (see *Hyperopisus*, p. 41), could be part of the sternohyoideus (see *Arapaima*, p. 15 and *Papyrocranus*, p. 20), or could be a separated segment of the hyohyoideus. Without ontogenetic studies it seems unlikely that an answer can be provided.

The *sternohyoideus* (text-figs 20 & 21) is a large muscle originating almost entirely from the dorsal face of the cleithrum, but with a few ventral fibres contributed by the hypaxial body musculature. Each ventral process from the second hypobranchial is very large, stout, and orientated so as to lie horizontally along and within the upper border of the sternohyoid (see fig. 21). Because the cleithrum is almost vertical in position and without a forwardly directed arm, the ventral processes form the ventral margins to the branchial chamber; in mormyrids the dorsal surface of the horizontal arm of each cleithrum forms the margin. The great size and peculiar orientation of the ventral processes in *Gymnarchus* appears to be unique within the Mormyriformes.

Ventral gill arch muscles in *Gymnarchus* conform to the usual mormyrid pattern but show several modifications doubtless associated with the reduced branchial skeleton in this genus (Taverne, 1970; Nelson, 1968).

The *obliquus* of the first gill arch is a stout muscle with a double insertion onto the anterior and posteroventral margins of the ceratobranchial; its origin covers most of the ventral surface of the hypobranchial. The second obliquus is a much smaller muscle. There is no obliquus muscle on the third arch, whose ceratobranchial is closely associated with the *rectus communis* muscle linking the fourth ceratobranchial with the base of the ventral process from the second hypobranchial.

The *pharyngocleithrales* are relatively stout muscles which can only be seen after deep dissection because they originate on the medial side of the sternohyoid (*cf.* mormyrids where the origin is lateral to that muscle). The near vertical cleithrum also effects the alignment of these muscles which thus originate behind the fifth ceratobranchial.

The internal muscle of each pair is the larger and longer; it runs obliquely forward and upwards to insert on the ventral tip of the ceratobranchial. The external

muscle is flatter and thinner, and runs almost vertically upwards to insert on the ventral face of the bone near its median edge and posterior border.

The *transversus* of the fourth arch is a fairly broad muscle linking the ventral tips of the ceratobranchials. The transversus of the fifth arch, however, joins the ceratobranchials near their posterior (*i.e.* upper) borders, and is in close contact with the external pharyngocleithrales near their points of insertion. This arrangement contrasts with that in the Mormyridae, where the fifth transversus runs forwards and medially as a V-shaped muscle to attach to the cartilaginous basibranchial plate between the fourth and fifth arches.

SUMMARY AND DISCUSSION

For the purpose of this discussion, the term ventral hyoid musculature includes the anterior and posterior intermandibulares, and the interhyoideus muscle (with its subdivisions), either as separate entities or with some elements partly fused to form a protractor hyoideus (see Introduction, page 4). My use of the term protractor hyoideus differs somewhat from that employed by Edgeworth (1935, p. 101). This implies neither criticism nor acceptance of Edgeworth's concepts, and is used merely for brevity's sake (but see page 49 below).

Among the Osteoglossomorpha, two principal types of ventral hyoid musculature can be recognized. In one there is a protractor hyoideus (Hiodontidae, Osteoglossidae and Pantodontidae), while in the other the posterior intermandibularis and the interhyoideus muscles are quite separate (Notopteridae and Mormyridae). *Gymnarchus* could, perhaps, be considered as constituting a third type, but I would prefer to consider its pattern as a modified mormyrid type (see below).

The pattern shown by *Hiodon* is the most unspecialized one, and compares closely with that of the holostean *Amia* and such primitive teleosts as *Elops* and *Megalops*. Compared with the protractor hyoideus in these fishes, that of *Hiodon* is a little more specialized because the component muscles show a greater degree of consolidation and unification (see page 9).

Apart from some slight intergeneric variations, the protractor hyoideus in the Osteoglossidae and Pantodontidae presents a uniform picture. Compared with *Hiodon*, consolidation of component muscles is carried even further. The compound muscle is, indeed, like that occurring in species of several euteleostean groups (*e.g. Salmo, Abramis* and *Peristedion*: see Edgeworth, 1935). Edgeworth (*op. cit.*), based on Holmquist's (1911) studies, interprets the ventral hyoid muscles in *Osteoglossum* as having the posterior intermandibularis " . . . attached by intersection to the inner part of the Interhyoideus, so that externally there is an Interhyoideus which reaches the jaws and internally a Protractor hyoidei". This description certainly fits the condition found in *Pantodon* (see page 16), but in the other osteoglossoid genera (including *Osteoglossum*) I can find no such clear-cut division into ventrally placed posterior intermandibularis and dorsal interhyoideus (see page 12). The impression gained is one of greater fusion between the two muscles (if indeed

they are arranged in a dorsoventral series). From adult anatomy it seems that an anteroposterior fusion is just as probable, the forward section being derived from the posterior intermandibularis muscle, the hinder part from the interhyoideus (see page 12). In other words, a condition fulfilling Edgeworth's definition of " . . . a fully developed Protractor hyoidei . . . —a longitudinal muscle the anterior part of which is formed by the Intermandibularis posterior and the posterior part of the Interhyoideus".[1]

The unconsolidated ventral hyoid muscles in notopterid and mormyrid fishes represent a different line of specialization, and one apparently otherwise seen only in siluroid ostariophysans (see pages 18 & 25).

In both notopterids and mormyrids the most superficial muscle is the posterior intermandibularis. The Gymnarchidae have lost the posterior intermandibularis, and thus the superficial muscle is probably an expanded anterior intermandibularis (see page 44). In all three families the interhyoideus component is a deep muscle, relatively small in notopterids but enlarged (and generally subdivided) in mormyrids and gymnarchids. There is also a difference in the way in which the interhyoideus inserts. Notopterids have the insertion on the hypohyals, but in the two other families the muscle is attached to the medial face of the lower jaw.

There is little intergeneric variation in the hyoid musculature of notopterids but a considerable amount within the mormyrids, involving all elements, including the anterior intermandibularis muscle.

Recent studies on the anatomy and osteology of mormyrid and gymnarchid fishes all indicate that species of the genus *Petrocephalus* are probably the least specialized (see Nelson [1968] on branchial arches; Taverne [1968, 1969 and 1970] on osteology, and Orts [1967] on visceral and auditory anatomy). *Petrocephalus* is also outstanding for being the only mormyrid in which the interhyoid of each side remains undivided. Of the other ventral muscles in *Petrocephalus*, the posterior intermandibularis is well-developed and expansive, but the anterior intermandibularis is absent (or, possibly, fused with the posterior muscle; see page 37). The anterior intermandibularis is present in other genera with relatively unspecialized cranial characters, for example *Marcusenius* which closely resembles *Petrocephalus* in many respects. Thus, the absence of an intermandibularis in *Petrocephalus* may be a specialization.

Equally, the broad and expansive anterior intermandibularis found in *Mormyrus*, *Hyperopisus*, *Isichthys*, and *Gymnarchus* is probably a derived condition, as would be the lack of this muscle in *Gnathonemus* and *Campylomormyrus*, genera showing great specialization in jaw and snout form. The peculiar condition of the intermandibularis muscle (or muscles) in *Mormyrops* (page 38) is difficult to interpret, and is unlike either the *Mormyrus-Marcusenius* or the *Gnathonemus-Campylomormyrus*

[1]If such definite ontogenetic differences exist in the way a "protractor hyoideus" is formed, then there would be every justification for recognizing the end products by different names.

I am less impressed by the validity of Edgeworth's (*op. cit.*) two subdivisions for those fishes without a fully formed (*sensu* Edgeworth) protractor hyoideus (see Edgeworth, *op. cit.*, pp. 100–101). For instance, the differences described by Edgeworth between *Perca* (his division 1) and *Osteoglossum* (division 2) seem to be more a difference of degree than of fundamental organisation.

types. The relatively short anterior intermandibularis of *Marcusenius* and *Cyphomyrus* should probably be taken as the least specialized mormyrid condition. Nevertheless, this type still represents a marked departure from the basic teleostean condition (as in *Hiodon*) or even that in the generality of the euteleosts.

The posterior intermandibularis is, in most mormyrid genera, well-developed and expansive. Although this form represents a derived condition as compared with the presumed basal teleostean type (*e.g. Hiodon* and *Elops*), it should probably be considered the primitive condition for mormyrids. Specialization by reduction of this state is seen in *Mormyrops, Isichthys* and *Hyperopisus*. This shared specialization cannot alone be taken to imply any phyletic relationship between these genera, especially since the end-product in *Mormyrops* is unlike that of the other two genera. Different specializations of the posterior intermandibularis are seen in *Gnathonemus* (extension in connection with the hypertrophied mental barbel, see page 32) and *Campylomormyrus* (multiple sites of origin, presumably correlated with extreme snout elongation and decurvature; see page 33).

The complete absence of a posterior intermandibularis in *Gymnarchus* is unique among mormyroid fishes, and is associated with a number of other muscular specializations in the hyoid and branchial systems (see page 44). The hyoid and gill arch musculature in this genus are so specialized that they provide few clear-cut phyletic pointers. About all that can be said regarding the relationships of *Gymnarchus* is that the presence in the skull of lateral ethmoids, paired orbitosphenoids, and a basisphenoid (see Taverne, 1970), together with the relatively unspecialized inner ear (Orts, 1967), all point to derivation from the *Marcusenius–Petrocephalus–Mormyrus* assemblage rather than the *Gnathonemus–Isichthys–Mormyrops* group.

The sum of characters, both specialized and generalized in *Gymnarchus* suggest that it was a fairly early departure from the main mormyroid stem. Its retention in a distinct, monotypic family is probably not justified on phyletic grounds; its placement in a subfamily (Gymnarchinae) of the Mormyridae, however, would more accurately reflect its relationships.

The ventral branchial muscles in the Osteoglossomorpha are, on the criteria discussed by Nelson (1967), moderately specialized, being comparable with those of *Polymixia* in his series *Elops–Aulopus–Polymixia–Epinephalus*. The presence of obliqui inferiores in the dorsal branchial musculature of mormyrids and osteoglossids is, according to Nelson (1969), a secondary and advanced feature not present in any member of his *Elops–Epinephalus* series.

In Nelson's argument, the development of a rectus communis (and the degree of its antero-posterior extent) is taken to be indicative of specialization. This muscle in Osteoglossomorpha provides something of a puzzle. It is developed in all members of the superorder except in three of the five osteoglossid genera, namely *Osteoglossum, Scleropages,* and *Arapaima.*[1] When present the muscle extends from the fourth arch to the second (attaching to the basibranchial in *Hiodon* but to the hypo-

[1]Hence, because these were the species he examined, Nelson's (1969) observation that a rectus communis is not developed in Osteoglossidae; it is, on the other hand, well-developed in *Heterotis niloticus* and *Pantodon buchholzi*.

branchial in all others). In terms of its volume, the muscle is largest in *Hiodon* although its anterior third is entirely tendinous.

Apart from the large rectus communis, the ventral branchial muscles in *Hiodon* show no outstanding characters. As in the notopterids (except *Xenomystus*) and osteoglossids, *Hiodon* has a rectus muscle between the third ceratobranchial and the second hypobranchial, and the well-developed pharyngocleithrales originate medial to the sternohyoideus.

An interesting feature of the notopterids is the way in which the heads of the ventral obliqui muscles on the first two arches attach to both the basibranchials and hypobranchials. The same muscles in mormyrids also have a complex origin, the first attaching to the second hypobranchial as well as to the first, and the second obliquus extending below the hypobranchial of that arch to reach the second basibranchial.

No rectus muscle is developed in mormyrids, but in one species (*Cyphomyrus discorhynchus*) a stout muscle links the ventral ends of the second and third ceratobranchials. Another peculiar muscle, present in most mormyrids (but not in *Mormyrops*, *Hyperopisus* or *Gymnarchus*, and weak in *Isichthys*) extends between the ventral ends of the fourth and fifth ceratobranchials (see page 26). This muscle could be a segment of the anterior transversus muscle. The posterior transversus in all mormyrids except *Gymnarchus* (page 48) is V-shaped with its apex attached to the cartilaginous fourth basibranchial.

The mormyrid pharyngocleithrales are, in general, weak and often tendinous muscles with a deep insertion onto the fifth ceratobranchial, and an origin lateral to the sternohyoideus. *Gymnarchus*, by contrast, conforms with the more usual teleost condition in which the muscles originate lateral to the sternohyoid.

All Osteoglossomorpha, with the exception of *Hiodon*, have a pair of ventrally directed bony processes associated with the ventral end of the second gill arches (see Greenwood *et al.*, 1966 and Nelson, 1968). The processes are closely associated with the sternohyoideus muscle to which they are closely attached or in which they are embedded.

The sternohyoid of *Hiodon* is particularly interesting in this regard, and suggests a way by which the typical osteoglossomorph hypobranchial process might have evolved. In *Hiodon* the main body of the sternohyoid arises, aponeurotically, on the hypaxial body muscles and is ventral to the cleithrum. A small dorsal part of the muscle on each side, however, originates from the cleithrum. Like the ventral part, it inserts of the urohyal, but from its middorsal region a broad slip of near-tendinous muscle runs forwards and inserts on the second basibranchial (fig. 4). The possible significance of this unusually discrete connection is best appreciated when one recalls the ventral processes (or tendon bones) in notopterids. In these fishes the tendon bones articulate with the second basibranchial (and not the hypobranchial as in other osteoglosomorphs), and are closely attached to the dorsal part of the sternohyoid.

The sternohyoid in Notopteridae originates entirely from the cleithrum. Its insertion is unusual since it has tendinous connections both with the hypohyals and

with the ceratohyals; furthermore, the muscle completely surrounds the small urohyal. Since the urohyal has strong ligamentous connections with the basibranchial tooth plate, the sternohyoid has connections, albeit indirect, with that bone as well.

Among the osteoglossids there is some fairly marked variation in sternohyoideus relationships. In all genera, however, the ventral hypobranchial processes are firmly attached to the muscle, which is also closely associated, by connective tissue fascia, with the first hypobranchials. *Arapaima gigas* has a complex sternohyoid (see page 15), subdivided into paired anterodorsal and unpaired ventral portions, the former inserting, through a common tendon, mainly onto the left ceratohyal. It is interesting to note that *Heterotis* (the other member of the subfamily Heterotinae) shows incipient longitudinal division of the sternohyoid anterodorsally (see page 14).

The mormyrid sternohyoideus shows little intergeneric variation, except in the relative proportions of the muscle originating from the cleithrum and from the hypaxial body musculature. All genera have a close association, through membranous fascia, between the muscle and the second basibranchial, and with the ventromedial elements of the first two gill arches (including, of course, the bony processes of the second hypobranchials).

The most outstanding feature of the sternohyoid in *Gymnarchus* is its relationship with the hypertrophied ventral processes. These elongate and robust bones are no longer ventrally directed, but lie horizontally and are embedded in the dorsolateral margin of the muscle (see page 47). The peculiar ceratohyal–urohyal muscle in *Gymnarchus* (see page 46) may be another specialization of the sternohyoid, but the relationships of the two muscles are still far from clear.

The hyohyoideus muscles in all Osteoglossomorpha, except the Mormyridae, conform to the usual teleost pattern.

The Mormyridae are outstanding for the extent to which the hyohyoidei are hypertrophied and so arranged that the "branchiostegal membrane" is virtually immovable (see page 23). The branchiostegal rays are deeply embedded in the thick superior hyohyodei which, in turn, are aponeurotically connected in the midline and are broadly inserted along almost the entire length of the ceratohyals. Because the inner aspect of each "branchiostegal membrane" is attached to the skin covering the ventral body musculature above and medial to them, they completely occlude the ventral opening to the peribranchial chamber. As a result, this opening is greatly reduced in its vertical extent.

Although it is not possible to carry out a reliable functional analysis on the basis of morbid anatomy, the arrangement of the hyohyoideus and sternohyoideus muscles in mormyrids suggests the development of a strong branchial pump. As a means of ingesting small prey, such a device would accord well with the weak jaws, small mouth and "parasphenoid-basihyal bite" of these fishes (see Nelson, 1968).

As with other myological features, the hyohyoideus muscles in *Gymnarchus* depart markedly from the typical mormyrid type (page 46). In this genus, the branchiostegal membrane is free from the overlying skin of the body, and the hyohyoidei are

reduced to a few fibres between the branchiostegal rays. Furthermore, these muscles are continuous with the more dorsally located interhyoidei (see page 45). Since *Gymnarchus* is the only mormyrid lacking parasphenoid teeth and tooth-bearing dermal plates on the basibranchials, it is very likely that the differences in musculature are associated with different feeding methods. That the gape of the mouth is relatively much larger than in the Mormyrinae, may also be significant.

Phyletic relations within the superorder. The ventral gill arch musculature provides little information on this subject. The presence of a rectus communis in some osteoglossoids (see page 18) rather negates the importance of this character in the analysis of gill musculature given by Nelson (1969). Nelson, on the basis of evidence then available noted the presence of this muscle in notopterids and mormyrids, and its absence in osteoglossids.

The hyoid musculature, on the other hand, allows a clear-cut division to be made into fishes with a protractor hyoideus (Osteoglossidae and Pantodontidae), and those in which the posterior intermandibularis and the interhyoideus are distinct muscles (Mormyridae [including *Gymnarchus*] and Notopteridae). The Hiodontidae have a primitive teleostean type of hyoid musculature with respect to which both other types must be considered specialized, albeit along different lines. The osteoglossoid specialization is a common one among teleosts (see Holmquist, 1911; Dietz, 1912; Takahasi, 1925; and Edgeworth, 1935). The notopterid-mormyrid type has otherwise been recorded only in the catfishes (Siluroidei, Ostariophysi).[1] This siluroid type (Holmquist, 1911; Takahasi, *op. cit.*; Munshi, 1960; also personal observations on *Ictalurus nebulosus*, *Parasilurus aristotelensis* and *Bagrus docmac*) is basically like that of the notoperids, but its specializations are of a type not found in the latter fishes (or the mormyrids either) since they are associated with the mandibular barbels. Because, on so many characters, the siluroids are not allied to the osteoglossomorphs, the resemblance in hyoid musculature can only be convergent.

Convergence is an unlikely explanation for the similarities between notopterid and mormyrid musculature; the two groups are related in so many other characters (Greenwood *et al*, 1966; Nelson, 1968 and 1969).

The relationships of the mormyrid fishes within the Osteoglossomorpha are still uncertain. Greenwood *et al.*, (*op. cit.*), give the Mormyridae ordinal status coordinate with all the other osteoglossomorphs (including the Hiodontidae). McAllister (1968) preferred subordinal status, coordinate with the Osteoglossoidei and Notopteroidei, in an order (Mormyriformes) which excluded the Hiodontidae. In a paper reviewing gill arch skeletons within the Osteoglossomorpha, Nelson (1968) pointed out that most authors have given undue emphasis to certain mormyrid characteristics (especially the brain and electric organs). As a result of this stress on differences, the phyletic relations, he thought, are obscured by the hierarchical categories chosen for the Mormyridae. The gill arch studies made by Nelson led him to rearrange the osteoglossomorphs into two suborders in an order, the Osteo-

[1]Munshi's (1960) description of the clupeoid *Hilsa ilisha* gives the impression that, in this species too, the posterior intermandibularis is the principal (and most superficial) hyoid muscle. The interhyoideus, he notes, is absent. I have dissected a specimen of this species and find that, like other clupeoids (see Kirchhoff, 1958) the interhyoideus and posterior intermandibularis are fused to form a protractor hyoideus.

glossiformes. In one suborder (Notopteroidei) he placed those families in which there are either no ventral processes on the second gill arch (Hiodontidae) or the processes are tendon bones articulating with the second basibranchials (Notopteridae). In the other suborder (Mormyroidei) Nelson placed those families in which the processes are bony and fused with the second hypobranchials (Mormyridae, Gymnarchidae, Pantodontidae and Osteoglossidae). Nelson's later studies (1969) on osteoglossomorph infraorbital bones (and some other features) gave no grounds for altering his earlier classification.

I agree with Nelson's (1968) comments on the undue weight given to certain mormyrid characters, but I consider that other evidence indicates closer relationship between the notopterids and mormyrids than between the latter family and the osteoglossids. This evidence (some yet unpublished) is concerned mainly with specializations of the inner ear shared by the notopterids and mormyrids. A specialized inner ear also occurs in the hiodontids (see Greenwood, 1970; and unpublished). All three groups have an otophysic connection (of varying complexity) but none exists in the osteoglossids. Other indicators of relationship between the notopterids and hiodontids are discussed by Nelson (1969, p. 27).

The ventral hyoid musculature of *Hiodon* is too unspecialized to be of value as a phyletic indicator, but the shared specializations of this musculature in mormyrids and notopterids (see above, page 53) seems to reinforce other characters suggesting a relationship between these families. The very different specialization shown by the hyoid muscles of the Osteoglossidae and Pantodontidae implies that these families together represent a distinct lineage.

Until I have completed certain other studies on osteoglossomorph anatomy it would be premature to put forward a revised formal classification of the superorder. However, it seems very likely that any new classification will group (within a single order) the Hiodontidae, Mormyridae and Notopteridae in one category (probably subordinal) and the Osteoglossidae and Pantodontidae in a second, and coordinate category.

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